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Within-year and among-year variation in impacts of targeted conservation management on juvenile survival in a threatened population.

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Abstract:

1. Overall impacts of targeted conservation interventions on population growth rate (λ) will depend on within-year and among-year variation in exposure of target individuals to interventions, and in intervention efficacy in increasing vital rates of exposed individuals. Juvenile survival is one key vital rate that commonly varies substantially within and among years, and consequently drives variation in λ. However, within-year, among-year and overall impacts of targeted interventions on population-wide survival probabilities of potentially mobile juveniles are rarely quantified, precluding full evaluation and evidence-based refinement of interventions.
2. We applied multi-state mark-recapture models to eight years of ring-resighting data from a threatened red-billed chough (*Pyrrhocorax pyrrhocorax*) population to quantify within-year and among-year variation in juvenile exposure to a targeted intervention of supplementary feeding and parasite treatment, and to estimate efficacy in increasing juvenile survival probability. We then combined and up-scaled these estimated effects to evaluate the impact of the eight-year intervention on overall population-wide survival probability and resulting population size.
3. High proportions of surviving juveniles (>70%) were exposed to the intervention across the annual biological cycle in all years. Exposure was associated with higher short-term survival probabilities through the full annual cycle. Consequently, management increased estimated population-wide annual juvenile survival by approximately 0.14. However, such effects were only evident in cohorts with low overall annual survival.
4. Population models projected that these impacts on annual juvenile survival substantially reduced population decline, such that population size at the end of the eight-year intervention was approximately double that without management.

5. *Synthesis and applications*. Our results show how complex patterns of within-year and among-year variation in exposure and efficacy of targeted conservation interventions can arise and scale up to affect population-level outcomes. We demonstrate positive effects of a major intervention, but also highlight potential routes to improve efficacy, for example through more precise targeting of agricultural management actions in the context of among-year variation in environmental conditions.

Keywords:

Annual juvenile survival probability, evidence-based conservation, multi-state mark-recapture, population growth rate, red-billed chough, seasonal demographic variation, supplementary feeding

1. INTRODUCTION

Effective conservation of threatened populations requires identification and mitigation of key demographic constraints that limit population growth rate (λ), and requires thorough evaluation of management intervention efficacy (Hammers et al., 2015; Plard et al., 2020; Sarno et al., 1999; Sibly & Hone, 2002). However, identifying the causes and timing of demographic constraints, and implementing and evaluating targeted interventions, can be challenging. Not least, demographic constraints and magnitudes of responses to interventions could vary both within and among years, substantially affecting overall efficacy. Yet, such temporal variation, and its implications for optimal conservation management, are rarely explicitly quantified.

Despite increasing appreciation that vital rates commonly vary within years, and hence that constraints on λ can be temporally restricted (Flockhart et al., 2015; Guimarães et al., 2020; Rushing et al., 2017; Sergio et al., 2019), individual- and population-level responses to anthropogenic change, including management impacts, are typically evaluated on overall annual timeframes (Marra et al., 2015). For example, threatened populations are commonly thought to be food-limited (e.g. Amar et al., 2005; Plard et al., 2020), but even when interventions aim to remedy perceived seasonal variation in natural food supply, outcomes are often evaluated solely at the annual scale (e.g. Siriwardena et al., 2007). However, within-year variation in vital rates and management impacts could limit overall efficacy (Timberlake et al., 2019). For example, if management aiming to sustain high annual survival successfully increases survival early in the annual biological cycle but fails in subsequent months, then overall objectives may not be met. Similarly, if substantial mortality occurs before management takes effect in the annual cycle, then annual survival will be relatively low even if subsequent management increases survival probability of remaining individuals. Moreover, if mortality is primarily concentrated within specific time-periods,

there may be little benefit in implementing year-round management. Such constraints may also vary among years. For example, when environmental conditions limit vital rates, management may be more effective when conditions are poor (Hammers et al., 2015; Timberlake et al., 2019). Explicitly quantifying both within-year and among-year variation in vital rates, and in management efficacy in ameliorating demographic constraints, is therefore necessary for designing optimally targeted and cost-effective interventions.

Juvenile survival (i.e. survival after fledging or weaning) is one vital rate that commonly varies substantially both within and among years, and can consequently drive variation in λ (Gaillard et al., 2000; Koons et al., 2017; Reid et al., 2004; Wiens et al., 2006). Managing juvenile survival may therefore be important for conservation success (Ha et al., 2010; Manlik et al., 2016; Sarno et al., 1999). Yet, comparatively few conservation programmes explicitly target juvenile survival rather than other vital rates such as adult survival or breeding success (but see Ha et al., 2010; Zeoli et al., 2008). For example, supplementary feeding, a widely used conservation tool, is typically targeted at breeding adults and/or dependant young (e.g. González et al., 2006; Schoech et al., 2008). There are consequently few data on efficacy of supplementary feeding to increase juvenile survival, despite food limitation being a common constraint (e.g. Wiens et al., 2006).

Improved management consequently requires quantification of within-year and among-year variation in efficacy of targeted interventions in increasing juvenile survival. This is particularly challenging, especially when juveniles are mobile rather than territorial, and may move between unmanaged and managed areas at different times. Indeed, successful conservation will depend not only on the timing and magnitude of intervention impacts, but also on the proportion of individuals exposed to the intervention (Newey et al., 2010), which may vary temporally (Chamberlain et al., 2005). Juvenile movements may consequently underlie temporal variation in demographic constraints and management success. Quantifying

how impacts of local conservation interventions scale up to affect realised population-wide survival probabilities is then not straightforward, but is critical to understand overall impacts on λ.

One population of immediate conservation concern, that is threatened by low juvenile survival and subject to a corresponding targeted intervention, is the red-billed chough (*Pyrrhocorax pyrrhocorax*, hereafter 'chough') population inhabiting the island of Islay, Scotland (representing 87% of Scottish pairs in 2017). Islay's population decreased from ~95 to ~55 breeding pairs during 1986-2007, associated with agricultural change (Trask et al., 2020, Appendix S1). Analyses of long-term demographic data identified variation in juvenile survival as the main driver of population dynamics, which in turn was substantially explained by variation in food (tipulid larvae) abundance and weather (Reid et al., 2004, 2008). A substantial decrease in juvenile survival probability to ~0.1 in 2007-2009 (from ~0.42 pre-2007) then threatened population viability (projected $\lambda \approx 0.87$, Reid et al., 2011). This decrease resulted from low post-fledging survival in late-summer (July-September), attributed to low food availability (Reid et al., 2008, 2011, Appendix S1). Furthermore, post-mortem examinations revealed pathologically significant respiratory and alimentary tract parasite burdens, which may have exacerbated mortality (Trask et al., 2020; Appendix S1). Consequently, an emergency intervention comprising a targeted multi-year supplementary feeding programme (Bignal & Bignal, 2011), accompanied by antihelminthic treatment of visibly infected individuals (Trask et al., 2020), was enacted in key areas of Islay to try to prevent population extinction. To inform decisions to continue or refine this intervention, it is essential to quantify efficacy, and its variation within and among years, and hence evaluate overall population-level effects.

Such analyses must account for individuals' movements between managed and unmanaged areas within Islay and resulting temporal variation in management exposure, and

account for imperfect detection of individuals across time. This can be achieved using multi-state mark-recapture models (White et al., 2006). Conceptually, such models consider that individuals can move between managed and unmanaged 'states' between discrete encounter occasions, and allow simultaneous estimation of exposure probabilities and exposure-dependent survival probabilities for successive time intervals within years. Overall annual-level effects can then be calculated.

Accordingly, we applied multi-state mark-recapture models to eight years of intensive year-round resighting data from colour-ringed juvenile choughs to quantify variable juvenile exposure to management within and among years, and to estimate management efficacy in increasing within-year and annual juvenile survival. We then combined these estimates within matrix population projections to estimate overall impacts of the eight-year intervention on population size. We thereby provide the full, quantitative evaluation required to refine ongoing management.

2. MATERIALS AND METHODS

2.1 Management intervention and demographic monitoring

Supplementary feeding and parasite treatment protocols were designed to target juvenile choughs (Bignal & Bignal, 2011, Trask et al., 2020). Since juveniles typically move from natal territories to traditional communal foraging and roosting areas during the weeks following fledging (Figure 1a; Bignal et al., 1997), interventions were targeted in these communal areas (Appendix S1). In brief, supplementary food was provided near-daily during the non-breeding season (typically late-June to mid-April; Figure 1a; Bignal & Bignal, 2011) during eight annual biological cycles (2010-2011 to 2017-2018) within two broadly defined areas (termed feeding-area-1 and feeding-area-2, Appendix S1). Quantities of food (primarily

157 mealworms and suet pellets with pinhead oatmeal) were limited, providing ~15% of
158 individual daily energy requirements (Bignal & Bignal, 2011). During 2014-2018, some
159 visibly infected individuals (signs of breathing difficulties, gaping with open bill, heading
160 shaking, coughing) were caught at supplementary feeding sites and treated with
161 antihelminthic (n=62 individuals, Trask et al., 2020).

162 Each May-June during 2010-2017, almost all chough breeding territories on Islay
163 were monitored, and samples of nestlings marked with unique colour-ring combinations
164 (n=550; 69±12SD nestlings/year, 24±4SD broods/year; ≥50% of nestlings fledged), allowing
165 subsequent field identification of known individuals (following Reid et al., 2004, 2011;
166 Appendix S1). Accordingly, the identities of colour-ringed individuals attending
167 supplementary feeding were recorded throughout the year; near daily in feeding-area-1, and
168 generally at least fortnightly in feeding-area-2. This generated high-quality, high-frequency
169 data on individual attendance (totalling ~35,000 resightings of juveniles; full details of
170 resighting regimes in Appendix S1). Extensive surveys were also undertaken across Islay,
171 providing resightings of individuals that did not attend feeding areas (totalling ~2,600
172 resightings of juveniles). Additionally, intensive resighting surveys were undertaken each
173 May during 2011-2018 (following Reid et al., 2011), resulting in very high annual resighting
174 probability across all age classes ($P \geq 0.98$), allowing accurate direct calculation of overall
175 first-year survival probability. As Islay's population is insular with no recent observations of
176 permanent emigration, estimates of local 'apparent survival' represent true survival.

177

178 **2.2 Mark–recapture modelling approach**

179 We used multi-state mark-recapture models to estimate transition probabilities (ψ) between
180 'states' that were or were not associated with the management intervention (see below), and

estimate state-, time- (within-year), and cohort- (among-year) dependent survival probabilities (S) alongside temporally- (within-year) and spatially-varying detection probabilities (p).

Resightings were used to create state-specific individual encounter histories for all 550 individuals colour-ringed in eight annual cohorts fledged during 2010-2017. To provide the temporal resolution required to quantify within-year variation in survival and movement, especially during and around the previously identified survival bottleneck in July-September (observed in 2007-2009; Reid et al., 2011), histories were compiled across the annual biological cycle, from May in each individual's natal year (i.e. ringing) to May the following year. They comprised ten defined encounter occasions (t_1-t_{10}) at which p was estimated, and hence nine intervals (i_1-i_9) over which S and ψ were estimated (Figure 1b). The first interval (i_1) corresponded to ringing to mid-June, followed by seven consecutive four-week (i.e. 28 day) intervals from mid-June until the end of December (i_2-i_8; Figure 1b). To maximise use of resighting data, 21- or 14-day encounter occasions within each interval were defined (Figure 1b, Appendix S3). Since survival during January-May was previously relatively high (Reid et al., 2011), and because there were limited resightings away from supplementary feeding areas during this period, the final 15-week period (i_9) was defined as one interval (Figure 1b). As S and p parameters for the final modelled interval and occasion may not be independently estimable from fully parameterised time-dependent models, an additional encounter occasion (t_{11}), and hence interval (i_{10}), was included, describing whether an individual was ever observed after age one year (Figure 1b). The resulting end S, p and ψ parameters are therefore nuisance parameters with no meaningful biological interpretation (estimates not reported), but mean that penultimate parameters that are of interest (for t_{10} and i_9) are fully identifiable.

For each encounter occasion (excluding t_1), observed individuals were assigned to one of three mutually-exclusive states based on their resighting location, and hence association with the intervention: at feeding-area-1 (hereafter 'State-Fed-1'), at feeding-area-2 (hereafter 'State-Fed-2'), or elsewhere (hereafter 'State-Unfed'). Here, 'Fed' and 'Unfed' are used to reflect the observation circumstances. However, since parasite treatment was non-random with respect to apparent condition, state and year (only visibly ill individuals attending feeding sites in certain years were treated), effects of feeding and parasite treatment cannot be separated (Appendix S3). Survival probabilities associated with State-Fed consequently represent joint effects of both. All individuals were assigned to State-Unfed at t_1 (ringing). Consequently, there was no estimable survival probability for State-Fed-1 or State-Fed-2 over i_1 (Figure 1c, Appendix S3).

2.3 Mark-recapture parameter constraints

As is inevitable for small populations of conservation concern, the small number of nestlings ringed each year (69±12SD, range 56-94) precluded effective estimation of all S, p and ψ parameters in a fully time- (within-year), cohort- (among-years) and state-dependent model. Parameter structures were therefore necessarily constrained to facilitate estimation of key parameters regarding management efficacy. Constraints were designed to group parameters within and among years, and between states, based on knowledge of the system and field protocols, and thereby pragmatically balanced model complexity with biological realism (forming a 'Test Model', Figure 1c, Appendix S3).

First, the eight cohorts were divided into two 'cohort-groups' that coarsely captured previously known among-year variation in annual juvenile survival probability calculated from the May surveys (Appendix S1). These cohort-groups comprised six 'poor-survival'

cohorts (2010, 2011, 2014-2017) which had low annual survival probability (mean 0.19±0.05SD, n=420 individuals), and two 'good-survival' cohorts (2012, 2013) which had higher annual survival probability (mean 0.38±0.02SD, n=130 individuals). This split allowed evaluation of among-group variation in management effects, while minimising within-group heterogeneity that would violate key mark-recapture model assumptions. Creating two groups (rather than more) was the best feasible approach to capture among-year variation while allowing reasonable parameter estimation given available numbers of marked individuals and cohorts. This cohort-group structure was used for S and ψ parameters but not for p (Figure 1c), since the consistent resighting efforts meant that state-dependent p was unlikely to vary substantially among cohorts.

Second, corresponding S and ψ parameters for juveniles at the two feeding areas (State-Fed-1 and State-Fed-2) were constrained to be equal, thereby effectively representing a single overall 'State-Fed'; Figure 1c). This reduced model was much better supported than a model with separate State-Fed-1 and State-Fed-2 parameters (Appendix S3). However, full state-dependence for p was retained to capture known spatial variation in resighting effort (Appendix S1, S3).

Third, within-year constraints on ψ and p parameters were set to capture known or postulated patterns of variation (Figure 1c, Appendix S3). Constraints on ψ parameters distinguished transitions to and from feeding-areas post-fledging (i_1) and at the end of the annual cycle (i_9), and around previously identified periods of variable survival (i_3-i_5, Figure 1c). They also allowed estimation of ψ between the two feeding-areas (i.e. between State-Fed-1 and State-Fed-2, Figure 1c; Appendix S3). Within-year constraints on p captured known temporal variation in resighting effort (Figure 1c; Appendix S3).

252 Finally, within-year constraints on S distinguished survival during the immediate-post
253 fledging period (i_1) and in July-September (i_3 and i_4), from that during early summer (i_2) and
254 late-autumn and winter (i_5-i_9, Figure 1c). The resulting Test Model contained 36 parameters
255 to be estimated (32 biologically meaningful, 4 nuisance, Figure 1c).

256

257 **2.4 Mark-recapture model analyses**

258 The Test Model was used to test hypotheses regarding impacts of management on occasion-
259 dependent survival probability for each state (Appendices S2, S3). Specifically, a series of
260 candidate nested models, where parameters of interest were constrained to be equal (for
261 example, S for State-Fed and State-Unfed for the same interval), were fitted and compared to
262 the Test Model.

263 Models were fitted using program MARK (White & Burnham, 1999), adjusting
264 survival estimates for uneven time intervals, and using Newton–Raphson optimization. The
265 Test Model showed little overdispersion, and hence little evidence of major lack of fit
266 (median variance inflation factor $\hat{c}$±SE: 1.17±0.01, Appendix S3). There was no evidence of
267 multiple maxima produced in the likelihood function (Appendix S3), implying that estimates
268 represent the global maximum of the likelihood.

269 Akaike's information criterion, corrected for small sample size and overdispersion
270 (QAICc), was used to assess relative support (Burnham & Anderson, 2002). Nested models
271 were considered better and less well supported than the Test Model, implying that focal
272 constrained parameters did not differ, if ΔQAICc <-2. Alternatively, nested models were
273 considered less well supported, implying that focal constrained parameters differed, if
274 ΔQAIC >+2. Full details of parameter estimates and model comparisons are in Appendix S3.

275

276 **2.5 Population-level effects**

277 To quantify overall impacts of the intervention on population-wide annual juvenile survival
278 (incorporating both exposure and exposure-dependent survival; Appendix S2), state-
279 dependent S estimates were weighted by the estimated proportions of individuals alive in
280 State-Fed versus State-Unfed at each occasion. These proportions were estimated by
281 calculating the probabilities of all 1023 possible pathways of exposure and survival through
282 the full annual cycle given state, within-year and among-year dependent S and ψ estimates
283 from the Test Model and associated error (Appendix S4). Overall population-level 'realised'
284 survival probabilities were then estimated as the sum of the products of all path probabilities
285 at each occasion (Appendix S4).

286 These 'realised' values were compared to a hypothetical 'worst-case' scenario with no
287 management, and a hypothetical 'best-case' scenario where all individuals experienced
288 management throughout the annual cycle. These two scenarios were respectively
289 parameterised by considering that all surviving individuals at t_2 either remained in State-
290 Unfed, or transitioned to and remained in State-Fed. To generate survival probabilities for
291 both scenarios, sequential estimates of S were multiplied to generate monthly and annual
292 survival estimates for 'poor-survival' and 'good-survival' cohorts separately. Approximate
293 95% confidence intervals (95%CIs; i.e. 2.5^{th}-97.5^{th} percentiles) for realised and hypothetical
294 scenarios were calculated by sampling 10,000 times from normal distributions of S
295 approximating estimates and 95%CIs from the Test Model (Appendix S5).

296 To explicitly estimate how intervention effects on juvenile survival alone affected
297 population size over the intervention period (2010-2017), we used pre-breeding census, birth-
298 pulse, stage-structured Lefkovitch matrix multiplications (Appendix S5). Three models were
299 parameterised using annual juvenile survival probability estimates from the three modelled
300 scenarios ('realised', 'worst-case', 'best-case'), accounting for the observed sequence of

301 'poor-survival' and 'good-survival' cohorts. Given the objective of evaluating population-
302 level consequences of management on juvenile survival, all other vital rates were set to
303 constant baseline values (Appendix S5). Associated 95%CIs were calculated as above, using
304 distributions of estimated annual juvenile survival.

305

306 **3. RESULTS**

307 **3.1 Resighting and transition probabilities**

308 Estimates of p varied within years and among states, reflecting known variation in resighting
309 effort (Figure 2a, Appendix S3). Values were always high for State-Fed-1, and for the May
310 survey (t_{10}, Figure 2a), generating sufficient power to estimate S and ψ parameters of interest.

311 Estimates of ψ from State-Unfed to State-Fed were high across the annual cycle,
312 particularly in 'good-survival' cohorts (Figure 2b,c). In contrast, ψ from State-Fed to State-
313 Unfed was generally low, as was ψ between the two Fed states (Figure 2b,c). Consequently, a
314 high proportion (>70%) of surviving ringed juveniles were exposed to management at each
315 occasion (Figure 3a,b). Only in the final occasion in 'good-survival' cohorts (Figure 3b) was
316 a majority of surviving individuals in State-Unfed, because of high ψ from State-Fed to State-
317 Unfed in i_9 (Figure 2c).

318

319 **3.2 Survival probabilities**

320 During the first interval after ringing (i_1), S was similar in 'poor-survival' and 'good-survival'
321 cohorts (Figure 2d,e; nested model better supported, ΔQAICc=-2.0, Appendix S3).
322 Furthermore, survival during i_2 did not differ between State-Fed and State-Unfed for either
323 'poor-survival' cohorts (ΔQAICc=-1.1) or 'good-survival' cohorts (ΔQAICc=-1.5). However,

S differed between State-Fed and State-Unfed through subsequent intervals, and furthermore, these differences differed between 'poor-survival' and 'good-survival' cohorts (Figure 2d,e).

For 'poor-survival' cohorts, S was low during i_3-i_4 (July-September) for both State-Fed and State-Unfed (Figure 2d), but was marginally higher for State-Fed (ΔQAICc=+1.5). S was then higher for State-Fed across intervals i_5-i_9 (September-May) compared to i_3-i_4 (ΔQAICc=+13.8), but remained similar for State-Unfed (ΔQAICc=-2.0, Figure 2d). Consequently, S during i_5-i_9 was considerably higher for State-Fed than for State-Unfed (ΔQAICc=+11.3). The low estimates of S for State-Unfed resulted in very low time-adjusted survival through the long interval between December and May (i_9).

In contrast, for 'good-survival' cohorts, there was little difference in S between State-Fed and State-Unfed (Figure 2e). Survival was similar in both states during i_3-i_4 (ΔQAICc=-2.0), and during i_5-i_9 (ΔQAICc=-1.9). However, S for State-Fed was still lower during i_3-i_4 than during i_5-i_9 (ΔQAICc=+3.8), while S for State-Unfed did not differ across these two periods (ΔQAICc=-1.5). This is because estimates for State-Unfed were very imprecise (Figure 2e), which is inevitable because high ψ to State-Fed in 'good-survival' years (Figure 2c) left few individuals in State-Unfed.

3.3 Population-level effects

Due to high ψ from State-Unfed to State-Fed and low ψ from State-Fed to State-Unfed (Figure 2b,c), and generally high S for State-Fed (Figure 2d,e), most surviving individuals at each occasion were in State-Fed, particularly in 'good-survival' cohorts (Figure 3a,b). In 'poor-survival' cohorts, the estimated 'realised' annual survival probability, which incorporated surviving individuals in both states at each occasion, was substantially greater than both the 'worst-case' scenario (Φ=0.16, 95%CI 0.13-0.20 versus 0.02, 95%CI 0.01-0.04,

Figure 3c asterisks), and the low survival observed during 2007-2009 (Φ=0.10, Reid et al., 2011) which prompted the management intervention. 'Realised' survival was, however, substantially lower than the 'best-case' scenario (Φ=0.26, 95%CI 0.21-0.32, Figure 3c asterisks). In 'good-survival' cohorts there was no difference between 'realised', 'worst-case' and 'best-case' scenario annual survival estimates (Φ=0.42 95%CI 0.34-0.50, Φ=0.40 95%CI 0.13-0.67, and Φ=0.41 95%CI 0.33-0.50, respectively), although the 'worst-case' estimates were again imprecise (Figure 3d).

Due to the positive estimated intervention effects in the 'poor-survival' cohorts (i.e. in six of eight years), the matrix models estimated that the intervention substantially reduced the decrease in population size that was otherwise projected to have occurred. Population size at the end of the eight-year period was predicted to be approximately double that without management (Figure 3e).

4. DISCUSSION

Quantifying within-year and among-year variation in exposure to management interventions in mobile individuals, and quantifying associated variation in exposure-dependent survival probabilities and resulting population-level impacts, is necessary to design efficient and effective management strategies. However, this is highly challenging. Our multi-state analyses of unusually high-frequency resighting data from a threatened chough population show that substantial proportions of ringed juveniles were exposed to an intervention, comprising supplementary feeding and targeted parasite treatment, during the annual cycle. Estimated survival probabilities were higher for exposed versus unexposed individuals, but only during certain periods within years, and in certain years. These estimated effects were

371 sufficient to slow the rapid projected population decline, but also reveal potential routes to
372 refine future management.

373 Since food limitation is likely to constrain survival probabilities and λ of many
374 threatened populations, supplementary feeding is a common intervention. Yet, while some
375 studies have quantified individual (Crates et al., 2016; Maggs et al., 2019) and spatial
376 (González et al., 2006) variation in supplementary food use, temporal variation in exposure is
377 rarely quantified or incorporated into assessments of overall management impacts. Our
378 analyses show high uptake of management throughout the annual cycle, highlighting the
379 value of prior knowledge of a population's natural behaviour and ecology in facilitating
380 targeted interventions. Given such high exposure, any increase in survival probability
381 associated with the intervention could increase population-wide survival probability and
382 hence population size.

383 In practice, realised population-level impacts of supplementary feeding programmes
384 are infrequently explicitly quantified (Ewen et al., 2014; Martínez-Abraín & Oro, 2013),
385 hindering evidence-based refinement. Our analyses show that, in years of lower overall
386 annual survival ('poor-survival' cohorts), survival probabilities early in the annual cycle
387 (July-September) were somewhat higher for individuals that experienced management than
388 those that did not, and were substantially higher through the subsequent winter-spring
389 (January-May). Low chough survival probabilities during July-September were previously
390 linked to low natural food availability, both on Islay (Reid et al., 2011) and Ouessant, France
391 (Kerbiriou & Julliard, 2007). Furthermore, among-year variation in annual juvenile survival
392 probability was previously tightly associated with winter tipulid larvae abundance (Reid et
393 al., 2008), implying that winter survival is also food-limited. Estimated increases in survival
394 probability in State-Fed may therefore directly reflect reduced starvation and/or parasite loads
395 due to the interventions. Alternatively, increases may arise through compound effects if

396 feeding increases individual condition sufficiently to improve parasite tolerance, and/or
397 reduces consumption of natural 'fallback' prey with higher parasite transmission risk.

398 However, during two years of higher observed annual survival ('good-survival'
399 cohorts), there was no evident difference in survival probability between defined Fed and
400 Unfed states, and hence no apparent effect of the intervention on juvenile survival. Studies on
401 other systems concluded that, as generally makes intuitive sense, supplementary feeding may
402 have less impact during periods of high natural food availability, when survival is not food-
403 limited (Ruffino et al., 2014; Sim et al., 2015). However, there are rarely data on natural food
404 availability to investigate this possibility. In our system, the two 'good-survival' cohorts
405 coincided with years of very high winter (post-fledging) tipulid larvae abundance, compared
406 to the six 'poor-survival' cohorts (means $2{,}215 \times 10^3 \pm 463 \times 10^3$SD and $876 \times 10^3 \pm 442 \times 10^3$SD
407 tipulids $ha^{-1}year^{-1}$ respectively, Appendix S3). The apparent lack of intervention impacts for
408 'good-survival' cohorts may therefore partly reflect better environmental conditions, resulting
409 in high estimated winter survival for individuals in State-Unfed. While winter tipulid
410 abundance cannot directly explain the lack of difference in survival between State-Fed and
411 State-Unfed in July-September, it may indicate some form of correlated environmental
412 conditions, such as availability of other invertebrate prey, or beneficial weather (Reid et al.,
413 2008).

414 However, since transition probabilities to State-Fed were higher in 'good-survival'
415 cohorts than 'poor-survival' cohorts, more individuals were exposed to the intervention and
416 very few individuals remained in State-Unfed. The higher annual survival probability may
417 therefore partly reflect these cohorts' higher exposure to the intervention. The interannual
418 (i.e. between cohort-groups) differences in transition probabilities could themselves reflect
419 differences in environmental conditions and/or associated social behaviour, but may mean
420 that intervention impacts on survival probabilities in 'good-survival' cohorts are undetectable

421 because so few individuals were in State-Unfed. Indeed, survival probabilities for State-
422 Unfed were estimated imprecisely, meaning that potential positive (or negative) intervention
423 effects cannot be definitively excluded. Nevertheless, since estimated survival probabilities
424 for the two states were near identical, the conclusion that they did not differ does not
425 necessarily reflect low power. There was consequently no conclusive evidence that the
426 observed increased exposure for 'good-survival' cohorts was solely responsible for their
427 higher annual survival probabilities.

428 Overall, our estimation that the targeted intervention increased juvenile survival,
429 primarily in years with low winter abundance of a key prey, supports the original inference
430 that juvenile chough survival is food-limited (whether directly and/or indirectly through
431 associated parasite exposure and social interactions). However, since the interventions were
432 implemented as emergency responses rather than controlled randomised experiments, exact
433 estimated effects, and inferences on underlying causes of variation, should be taken with
434 appropriate caution. Our analyses cannot account for potential intrinsic differences between
435 individuals that did and did not attend feeding areas at specific occasions. However, feeding
436 took place at three separate locations (Appendix S1), and attendance was not strongly
437 structured in relation to individuals' natal locations. The apparent positive effect observed in
438 the 'poor-survival' cohorts is perhaps intuitively unlikely to simply reflect quality, since
439 individuals with higher mortality risk might be expected to use the supplementary food most.
440 If that were true, our analyses could underestimate positive intervention effects. Nevertheless,
441 at face value, our estimates suggest that the intervention effects on juvenile survival were
442 sufficient to reduce (but not prevent) population decrease. Previous analyses showed that the
443 intervention also had substantial collateral benefits, by increasing adult survival probability
444 and components of reproductive success (Fenn et al., 2020). Together, these results imply

445 that the intervention successfully prevented a rapid population decline (Trask et al., 2019).
446 Indeed, observed population size has been approximately stable since 2014.

447

448 **4.1 Management implications and context**

449 Proactive conservation should ideally iterate through cycles of evidence-based design,
450 implementation and (re-)evaluation of targeted interventions (Sutherland et al., 2004), yet
451 comparatively few conservation-focused studies evaluate intervention efficacy (Williams et
452 al., 2020). Studies that do not evaluate variation in responses among seasons or years also
453 risk providing misleading assessments. Our results suggest that responses to targeted
454 supplementary feeding and parasite treatments are temporally variable, opening potential
455 routes to further increase efficacy and cost-effectiveness. For example, the remaining period
456 of low survival during July-September could potentially be further ameliorated by providing
457 more food during this relatively short period, and/or implementing parasite treatments sooner
458 after fledging. Since management had little detectable effect in some years, cost-effectiveness
459 could in principle be improved by evaluating survival rates in autumn each year, and
460 inferring whether food provisioning is warranted throughout the winter and spring.
461 Furthermore, since not all juveniles experienced management, overall efficacy could
462 potentially be increased through additional feeding sites. The current implementation was
463 facilitated by chough social behaviour, whereby most sub-adults congregate in relatively
464 discrete areas. Monitoring during the supplementary feeding programme has further
465 increased understanding of post-fledging behaviour, which may help identify additional sites
466 for future targeted feeding, although wider implementation may prove logistically difficult.

467 Nevertheless, while intensive conservation interventions are often required to slow or
468 prevent extinction of threatened populations (e.g. Oro et al., 2008), they are not necessarily

sustainable or desirable long-term. Supplementary feeding, and associated parasite treatments, should ideally only be enacted until habitat management to increase safe natural food resources is in place (Schoech et al., 2008). Long-term persistence of Scottish choughs will require targeted management initiatives that increase the availability, abundance, and spatial and temporal diversity of natural food in traditional chough foraging areas, particularly in key grassland and sand dune systems within nursery areas (Trask et al., 2020). Consequently, in common with other grassland bird species, effective, long-term conservation will ultimately rely on appropriate and effective land management programmes.

Authors' contributions

All authors contributed to conceptual development. S.R.F. and J.M.R. devised analyses. S.R.F. undertook analyses. E.M.B. and S.B. managed and undertook supplementary feeding and data collection, with contributions from D.I.M., J.M.R, A.E.T and S.R.F. S.R.F. wrote the manuscript with contributions from J.M.R, with input and final approval from all authors.

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493 **Data accessibility**

494 Data available via Dryad Digital Repository upon manuscript acceptance.

495

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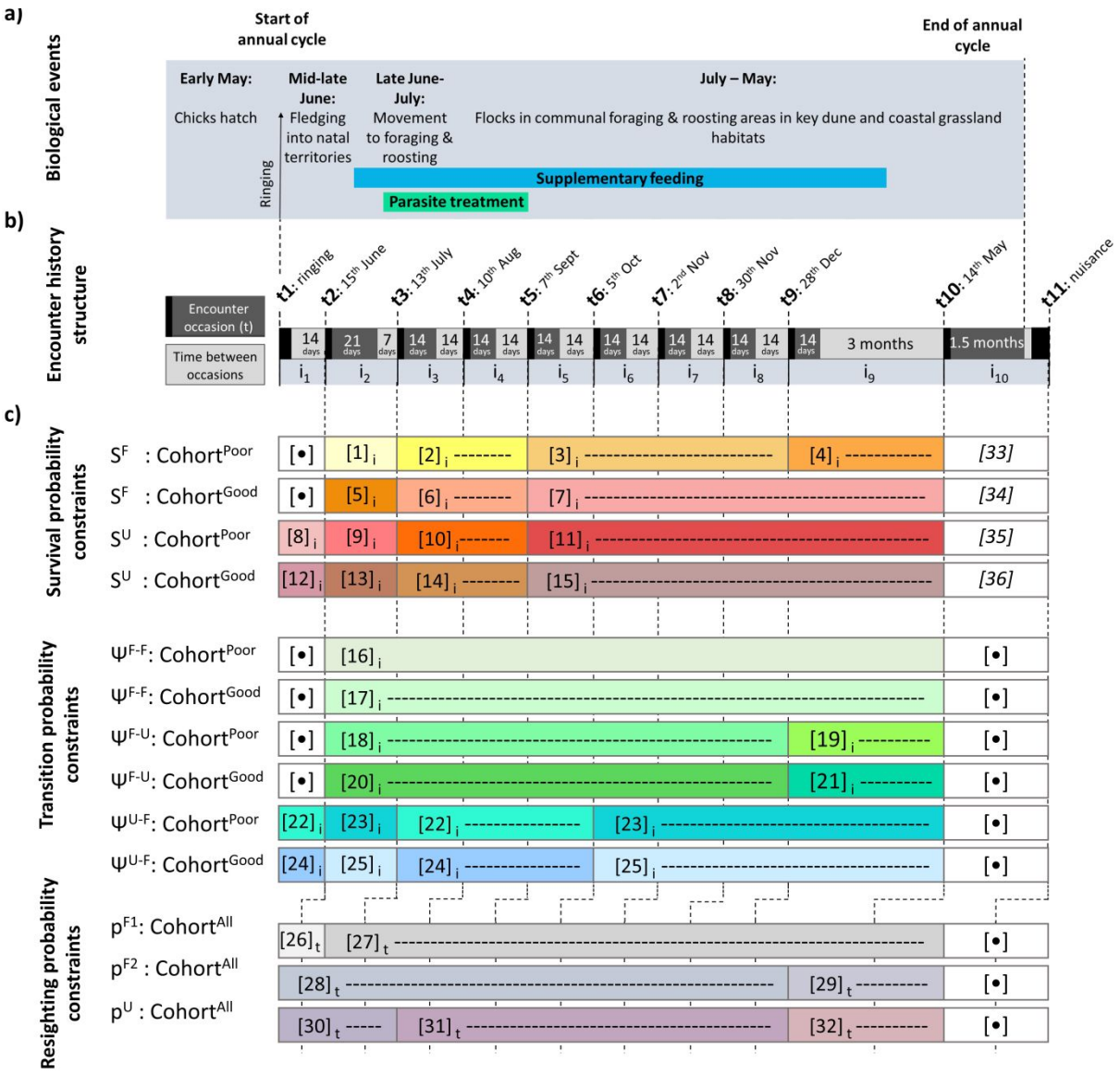

Figure 1: Structure of multi-state mark-recapture models used to estimate within-year and among-year variation in exposure to management and associated variation in juvenile survival. a) Summary timings of key biological and management events though an annual cycle. b) Encounter history structure, comprising 11 encounter occasions (t_1-t_{11}), and ten intervals (i_1-i_{10}) from colour-ringing in May. The final encounter occasion (t_{11}) is a nuisance parameter, describing whether an individual was observed after age one year; parameter estimates associated with t_{11} and i_{10} are not biologically meaningful. c) Within-year constraints on group-dependent ('poor-survival' or 'good-survival' cohorts) and state-dependent (F=Fed, U=Unfed) survival (S), transition (ψ)

and resighting (p) probability parameters in the 'Test Model' (full details, Appendix S3). The Test Model contained 36 parameters to be estimated, shown by numeric indices (32 biologically meaningful [S:[1]-[15], ψ:[16]-[25], p:[26]-[32]; 4 nuisance [*33*]-[*36*]), and highlighted by different colours. S and ψ parameters, and hence constraints, are associated with intervals (i), and p parameters are associated with encounter occasions (t). Other parameter ([•]) values were fixed (Appendix S3). For example, since all individuals start in State-Unfed at ringing, there are no estimated State-Fed survival probabilities over i_1.

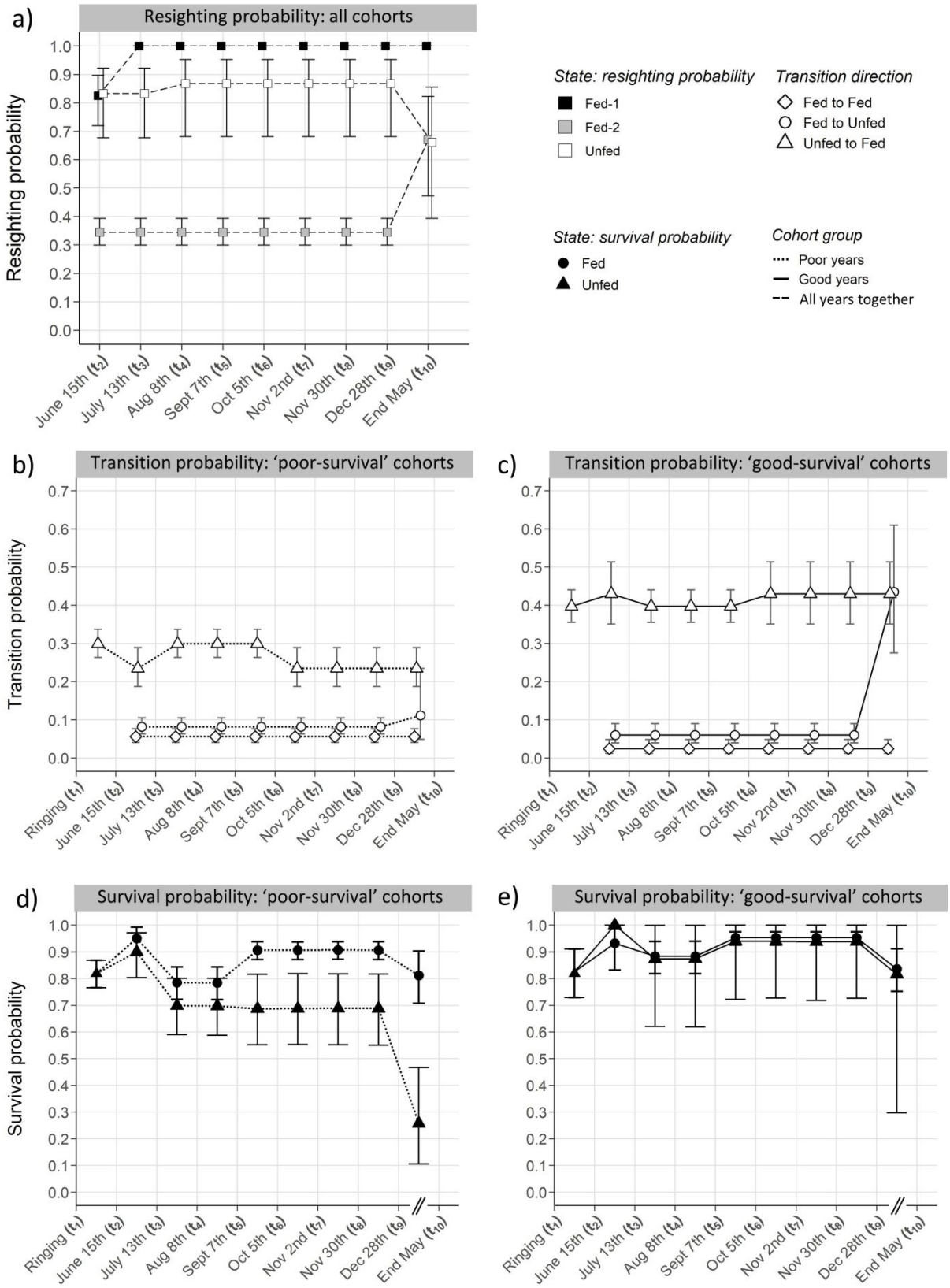

Figure 2: Test Model parameter estimates with 95% confidence intervals. a) State and time (within-year) dependent resighting probabilities. State, time and cohort (among-year) dependent b&c) transition and d&e) survival probabilities in 'poor-survival'

712 **(b&d) and 'good-survival' (c&e) cohorts. X-axis labels indicate the start date of each**
713 **encounter occasion or interval. Points (jittered to aid visualisation) show transition or**
714 **survival probabilities across corresponding intervals. The lower survival probability**
715 **during January-May reflects the long interval.**

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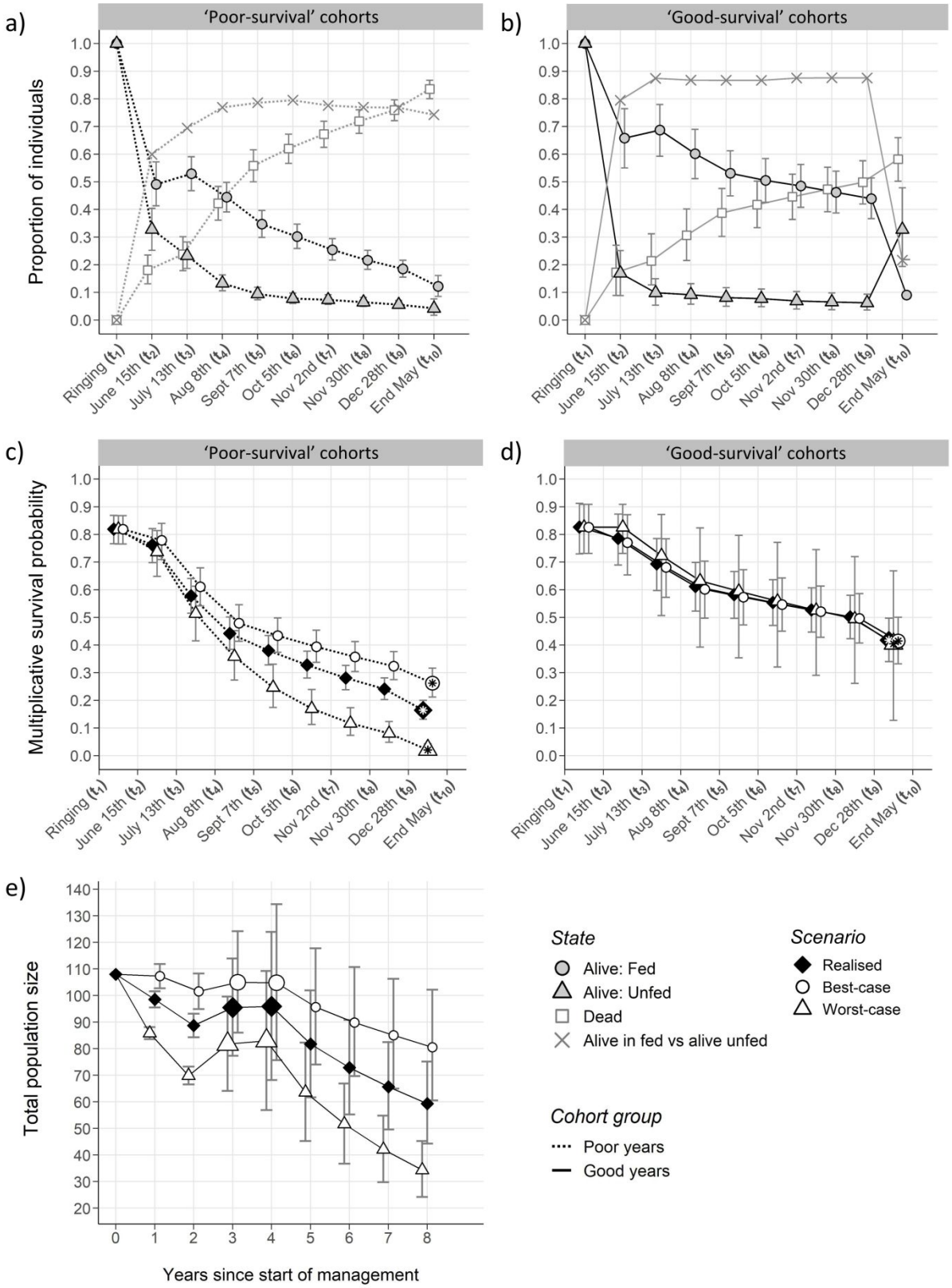

Figure 3: Derived estimates (with 95% confidence intervals) of management impacts from the Test Model. Time (within-year) and cohort (among-year) dependent proportion of individuals alive in State-Fed, alive in State-Unfed, dead, or alive in fed

versus alive in unfed in a) 'poor-survival' and b) 'good-survival' cohorts. Multiplicative 'realised' survival probabilities compared to hypothetical 'worst-case' and 'best-case' scenarios for c) 'poor-survival' and d) 'good-survival' cohorts (annual-level probabilities highlighted by final points with asterisks). e) Estimated total population sizes across the intervention period (2010-2018) for each scenario (small and large points show 'poor-survival' and 'good-survival' cohorts respectively). Points are jittered to aid visualisation.

Supporting information

Within-year and among-year variation in impacts of targeted conservation management on juvenile survival in a threatened population.

Sarah R. Fenn, Eric M. Bignal, Sue Bignal, Amanda E. Trask, Davy I. McCracken, Pat Monaghan and Jane M. Reid

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Appendix S1. Further details of study system and supplementary feeding

1.1 Further details of study system

Red-billed choughs (hereafter 'choughs') are a UK and European conservation priority species (Schedule 1 Wildlife and Countryside Act 1981, Annex 1 EU Birds Directive), which have declined throughout much of their European range in tandem with changing pastoral agriculture and livestock grazing practices, such as reduced cattle and sheep stocking intensities, and changing animal husbandry practices (Bignal et al., 1997). Changes in such practices can affect the availability and quality of suitable chough foraging habitats (e.g. Gilbert et al., 2019; Josson et al., 2020), and consequently may be linked to regional differences in population trends across the British Isles (Hayhow et al., 2018).

The Scottish population has been monitored since 1983 (Bignal et al., 1987; Reid et al., 2003, 2004, 2008) through colour-ringing and resightings, which allows estimation of age-dependent survival (Reid et al., 2003, 2004), and through comprehensive breeding surveys, which allows assessment of breeding success. The intensive, long-term monitoring (Reid et al., 2009; Trask et al., 2020) has facilitated identification of most potential nest sites, which are located in sea caves, farm buildings and in purpose-built field shelters (Hayhow et al., 2018), and are frequently re-used by pairs across years. Consequently, intensive surveys during each breeding season since 2004 have effectively covered most, or all, active chough breeding territories. Since choughs are a Schedule 1 species, nest site visits were kept to a minimum, and followed protocols designed to minimize disturbance to breeding pairs. As such, monitoring typically included an initial survey of all plausibly occupied territories to establish breeding pairs and breeding activity (i.e. stage of breeding: incubating versus with chicks), and then a single visit to a sample (≥50%) of accessible cave and building nest sites to colour-ring offspring (each individual given a unique combination of three colour-rings), typically when aged 15-25 days post-hatch.

Juvenile choughs fledge approximately six weeks post-hatch, and leave natal territories within a few weeks post-fledging (mid-late June) along with their parents to join sub-adult (i.e. pre-breeding) foraging and roosting flocks, which primarily occupy two traditional areas on Islay (Bignal et al., 1997). Adult choughs typically remain with young in these sub-adult flocks for some time, continuing to forage and feed their offspring for several weeks while juveniles learn to effectively forage for themselves. Adults then either return to their territories, or remain in the flock, but without maintaining direct care of offspring. Juveniles then remain in these sub-adult flocks year-round until acquiring breeding territories, typically aged 2-3 years (Bignal et al., 1997). All adults return to their territories each spring (March-May) for breeding, while sub-adult flocks remain in communal foraging and roosting areas.

Sub-adult flocking areas and breeding territories were monitored during months immediately post-fledging (June-July), thereby maximising both sightings of individuals that had moved to communal foraging and roosting flock areas, and of those that had not. Subsequently, most observation effort focused on flocking areas (and in years of the supplementary feeding programme, primarily at supplementary feeding areas), but occasional surveys outside these areas also produced sightings of individuals which were not observed in sub-adult flocks.

Previous mark-recapture analyses showed that juvenile annual survival varied considerably between years (Figure S1a), and identified key environmental drivers of juvenile survival (Reid et al., 2008), and a critical decline in survival between 2007-2009 to ~0.1 (Figure S1a; Reid et al., 2011) which prompted the emergency supplementary feeding intervention. Then, an updated mark-recapture analyses of age- and year dependent survival also showed that annual juvenile survival during the focal intervention period (2010-2018) also varied between years (Figure S1a), with years of lower survival (2010, 2011, 2014-2017;

here termed 'poor-survival' cohorts, average annual survival = 0.19±S.E. 0.02) and years of higher survival (2012 and 2013; termed 'good-survival' cohorts, average annual survival = 0.38± S.E 0.01).

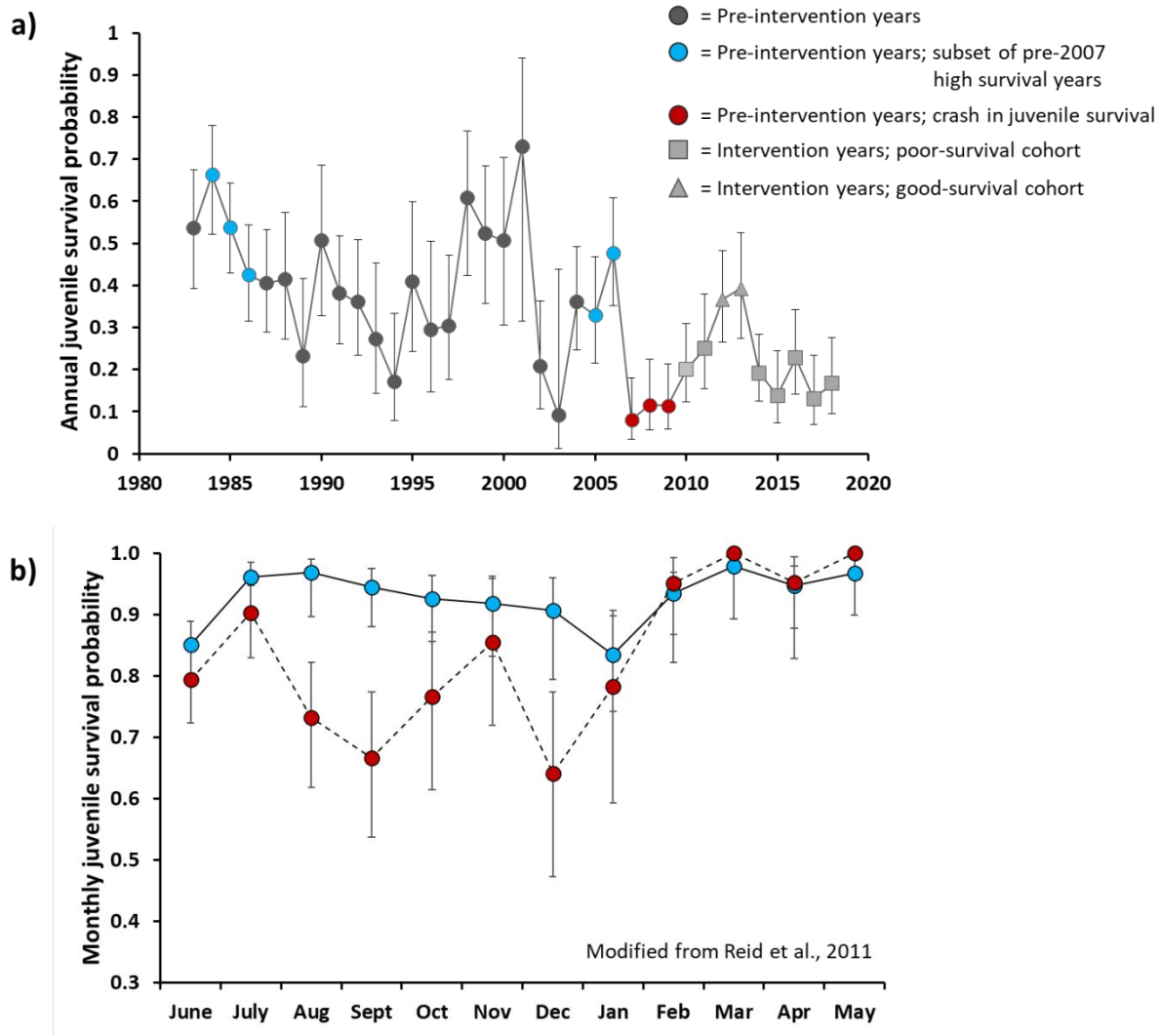

Figure S1: Estimated survival probabilities of juvenile choughs on Islay, Scotland (error bars: 95% confidence intervals) from previous published analyses. a) Annual juvenile survival probabilities, both before (circle points) and during (square and triangle points) the intervention period. Historically, survival was typically high (dark grey and blue points) but decreased substantially during 2007-2009 (red points). Annual survival probabilities during the intervention period varied, with years of lower survival (squares; 'poor-survival' cohorts, average annual survival = 0.19±S.E. 0.02) and years of higher

survival (triangles; 'good-survival' years, average annual survival = 0.38± S.E 0.01). Points in blue and red identify years used in the analyses by Reid et al. (2011) that initially highlighted the within-year constraints on juvenile survival. b) Estimated monthly apparent survival probabilities from years prior to the intervention period (Reid et al., 2011), comparing a subset of years with high annual survival (1984, 1985, 1986, 2005, 2006; blue points) and low annual survival (2007–2009, red points). X-axis labels indicate the end of each survival period (hence 'May' indicates survival for April–May).

1.2. Supplementary feeding programme and parasite treatment

A trial supplementary feeding programme was implemented at one site during the winter (December-May) of 2009-2010 to test feasibility and develop methods to minimise change in the flock's natural behaviour (Bignal & Bignal, 2011; food-station-1 in Figure S2). Based on the success of this trial, supplementary food was provided between 2010-2011 and 2017-2018 (i.e. eight years) in the non-breeding season between late-June (i.e. post breeding) and mid-April the following spring (Trask et al., 2020). Food was not provided during the breeding season since there was no evidence that breeding success was food limited. Supplementary food was provided near daily in two areas (hereafter feeding-area-1 and feeding-area-2), at up to three sites (hereafter food-station-1, food-station-2 and food-station-3; Figure S2). Each of these food-stations covered a small area, under $25m^2$ each. Feeding-area-1 included both food-station-1 and food-station-3, which were grouped because feeding and resighting regimes were generally similar, but too few individuals typically attended food-station-3 to retain it as a separate group. While resighting effort differed between feeding-areas (Table S1), the total number of days on which supplementary food was provided each year was similar between feeding-area-1 and feeding-area-2. It was assumed (and supported by field observations) that most individuals that used the area surrounding the supplementary feeding at food-station-2 attended feeding, and so to maximise data

availability, sightings assigned to feeding-area-2 also included those from the immediate surrounding area.

Supplementary feeding commenced at food-station-1 in 2010-2011, and at food-station-2 in 2011-2012. Food-station-1 was near a known roost site, where sub-adult flocks foraged in the evenings prior to roosting (Bignal & Bignal, 2011). Food was provided here once a day in the evening before the birds went to roost. Food was provided at food-station-2 once a day during late morning to early afternoon in a sand blow-out used as a livestock burial area, where sub-adult choughs were regularly seen foraging. Supplementary food was first provided at food-station-3 in 2011-2012, but was only used temporarily when sub-adult choughs used the local area (i.e. food not provided on all days, months or years; Table S1).

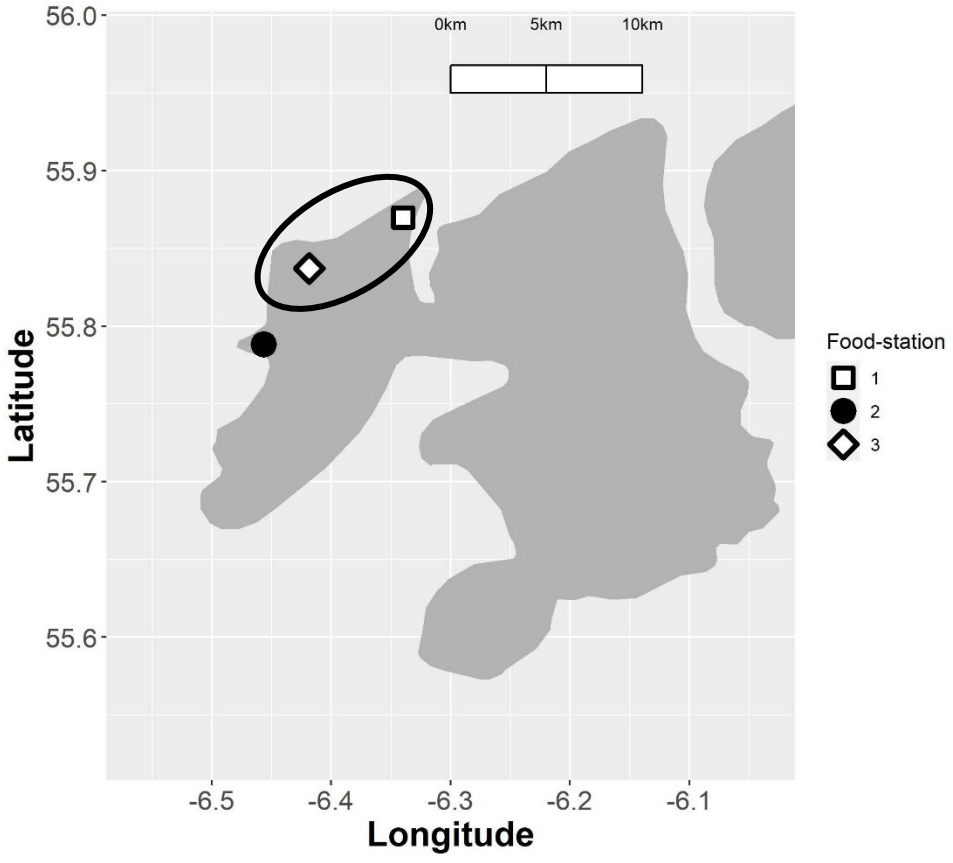

Figure S2: Supplementary feeding sites on Islay, Scotland. Fill of symbols indicate grouping of feeding stations into the two feeding areas, based on resighting efforts; feeding-area-1 (open symbols grouped by circle; high resighting effort sites), and feeding-area-2 (filled symbol; lower resighting effort site).

Supplementary food was not provided ad libitum to reduce the risk of dependence on artificial supplementary food sources (Bignal & Bignal, 2011; Trask et al., 2020). This protocol of limiting food quantity, and providing food at the time of day during which individuals would be naturally using the area, aimed to limit change in the natural behaviour of the sub-adult flock, as well as reduce the risk of disease transmission through attracting non-target species, such as rooks (*Corvus frugilegus*) and jackdaws (*Corvus monedula*). The feeding sites were further managed to reduce potential risk of disease and parasite transmission between birds by utilising sandy areas (where key intermediate parasite host species are less likely to be found), and regular replacement of the underlying sand; there was no evidence to suggest that supplementary feeding was linked to parasite burden (Trask et al., 2020).

Table S1. Total number of days that supplementary feeding and recording of attending colour-ringed choughs were carried out at the three supplementary feeding sites, and total number of resightings of attending colour-ringed choughs during each non-breeding season. Supplementary food was not provided at all sites in all years (i.e. number of days of supplementary feeding = NA). *At food-station-2, colour-ring resightings were not carried out every day that supplementary food was provided. The total number of days on which food was provided was similar to that at food-station-1.

Non-breeding season	Number of days of supplementary feeding and colour-ring resighting at each food-station (FS)			Total no. of colour-ring resightings
	FS-1	*FS-2**	*FS-3*	
2010-2011	228	NA	NA	5603
2011-2012	244	29	39	8979
2012-2013	295	30	233	13017
2013-2014	246	32	200	12313
2014-2015	296	25	NA	16852
2015-2016	215	23	274	11304
2016-2017	252	44	NA	9878
2017-2018	259	44	65	9507

154

155 To allow estimation of survival probabilities of individuals that did not attend feeding
156 areas, which was necessary to evaluate supplementary feeding effects on survival, extensive
157 resighting surveys away from feeding areas were also undertaken (see also Methods of main
158 text). Other key chough foraging areas outside of those immediately surrounding the feeding
159 sites were surveyed as feasible throughout the year across the duration of the study period.

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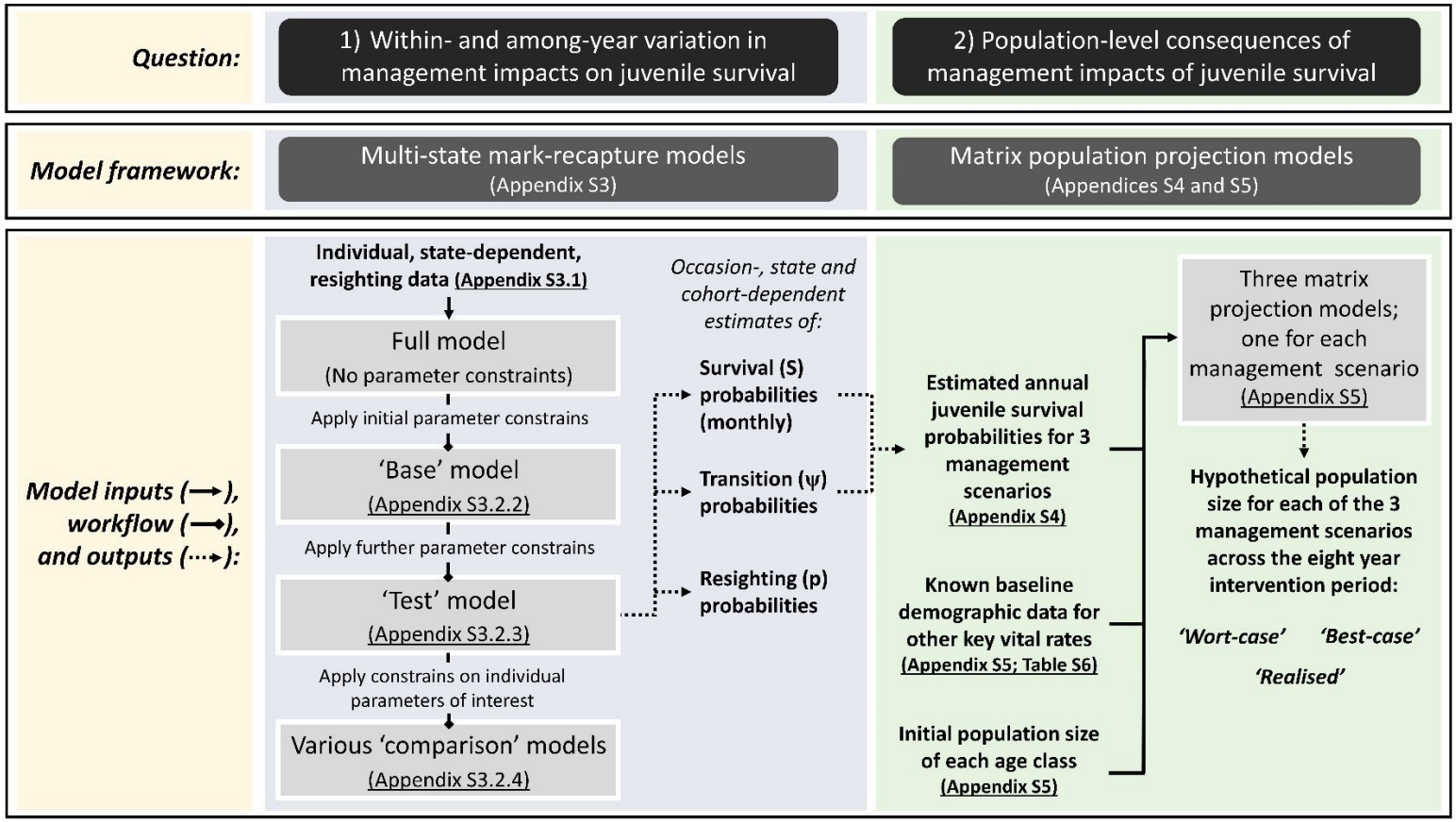
166 **Appendix S2. Graphical overview of analysis workflow**



167

168 **Figure S3: Summarised conceptual workflow of analyses, with model data inputs (solid arrows) and outputs (dashed arrows),**

169 **progression between stages of multi-state mark-recapture analyses (clubbed arrows), and progression from estimates of survival and**

170 **transition probabilities from multi-state mark-recapture analyses into matrix population projection models.**

171 **Appendix S3. Details of multistate mark-recapture modelling methods**

172 Data from the trial supplementary feeding programme during winter 2009-2010 (Bignal &
173 Bignal, 2011) were excluded from current analyses of juvenile survival; as supplementary
174 feeding only began in late December, this was not comparable to years where management
175 encompassed the whole non-breeding season. Analyses were therefore restricted to the 2010-
176 2017 cohorts.

177

178 3.1 Data formatting: encounter histories and states

179 *3.1.1 Encounter history structure*

180 Individual encounter histories were compiled from May in each individual's natal year (i.e.
181 ringing) to May the following year, and comprised ten defined encounter occasions (t_1-t_{10}),
182 and hence nine intervals (i_1-i_9) over which survival probability was estimated, plus an
183 additional 'nuisance' occasion and interval to allow parameters for t_{10} and i_9, which are of
184 interest, to be fully identifiable (Figure 1 in main manuscript). Individual encounter histories
185 were therefore coded by 11 encounter occasions. Unequal interval lengths were specified
186 directly in program MARK (i_1-i_{10} lengths specified as 2, 4, 4, 4, 4, 4, 4, 4, 15, 5). Therefore,
187 survival parameters gave estimates of weekly survival probability, which were scaled back to
188 the true interval length.

189 Hatching and ringing dates vary between nests, and so the length of the first interval
190 (i_1), which described the time from ringing to mid-June, is not the exact same across all
191 individuals. For purposes of modelling however, the length of the time interval was defined
192 as 14 days (Figure 1, main manuscript).

193 Mark–recapture models assume that the length of encounter occasions is negligible
194 relative to that of the interval between occasions, and therefore that no mortality occurs

during the encounter occasion (the recapture duration assumption). However, to maximise data availability, particularly of individuals associated with supplementary food-station-2, and individuals not attending supplementary feeding, relatively lengthy encounter occasions were used here (Figure 1, main manuscript). However, O'Brien et al. (2005) found that violating the recapture duration assumption to increase sample size increased precision, but not bias, in parameter estimates. Therefore, relaxing the recapture duration assumption and using an encounter occasion that maximises sample size and resighting probability in this study is unlikely to substantially bias results. Furthermore, since there were no recent observations of accidental ring loss on juveniles (i.e. no observed losses of one or two of the three colour-rings given to each individual), the mark-recapture model assumption that marks are not lost was met.

3.1.2 Feeding states

At an encounter occasion, individuals were either unobserved, or observed in one of three different states, based on the geographic location and activity associated with their colour-ring resightings; State-Fed-1 (resighted in feeding-area-1), State-Fed-2 (resighted in feeding-area-2), or State-Unfed (resighted elsewhere); see Table S2 for an example. Individuals observed at a feeding station were regarded as in a Fed state, regardless of food quantity consumed. While observations indicated that some individuals consumed more food than others, the key assumption for current analyses, that individuals in State-Fed on average consumed more supplementary food than individuals in State-Unfed, is valid.

There were very few instances (N<10) where an individual was observed in multiple states within a single encounter occasion. Since multi-state models require observed individuals to be assigned to a single state at each encounter occasion, these few individuals

were randomly assigned to one observed state, weighted towards the state in which it was observed most frequently.

Table S2: Example juvenile encounter histories. 0=not observed; F1=State-Fed-1, observed feeding at food-station-1 or food-station-3; F2=State-Fed-2, observed feeding at food-station-2 or close surrounding area; and U=State-Unfed, observed, but not associating with a food-station. The first occasion that individuals are encountered (t_1) marks colour-ringing, and so all individuals started in State-Unfed. The last occasion that individuals could be encountered in (t_{11}) was a nuisance parameter describing observations past the first year of life; all individuals observed at t_{11} were assigned to State-Unfed. Through the intervening encounter occasions (t_2-t_{10}), observed individuals could be assigned to State-Fed-1, State-Fed-2, or State-Unfed, based on location of observations.

Individual	Cohort	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}
1	2010	U	U	F1	U	F1	F1	F1	F1	F1	F1	U
2	2010	U	U	0	0	U	0	0	0	0	0	0
3	2011	U	0	F1	F1	F1	F1	F1	F1	F1	F1	U
4	2011	U	U	U	F2	U	U	U	U	0	0	0
5	2012	U	U	F1	F1	0	0	0	0	0	0	0
6	2014	U	0	F2	0	0	F2	F2	0	F2	0	U
7	2014	U	0	0	0	0	0	0	0	0	0	0
8	2016	U	0	F2	0	0	0	0	0	0	0	0
9	2016	U	F2	F2	0	0	F2	0	F2	F2	F2	U
10	2016	U	0	U	F1	F1	F1	F2	0	F2	F2	U

233

234 3.2 Model fitting and selection process

235 Model parameter constraints between cohorts are described in the main text (Figure 1), and
236 further details of constraints placed on survival (S), resighting (p) and transition (ψ)
237 probabilities are described below, and in Figure S5.

238

239 *3.2.1 Cohort-group structure*

240 The split of the eight cohorts into the two defined 'cohort-groups' ('poor-survival' and 'good-
241 survival') was necessarily defined *a priori* to coarsely capture known among-year variation in
242 annual juvenile survival probability, and thereby minimise within-group heterogeneity that
243 would violate key mark-recapture model assumptions.

244 However, these 'poor-survival' and 'good-survival' cohort-groups also corresponded
245 to years of lower and higher winter tipulid larvae abundance in the winters post-fledging
246 (means $876x10^3 \pm 442x10^3$SD $ha^{-1}year^{-1}$ and $2{,}215x10^3 \pm 463x10^3$SD $ha^{-1}year^{-1}$ respectively,
247 Figure S4). This implies that among-year variation in annual juvenile survival probability,
248 and hence the defined cohort-groups, may at least partly reflect underlying environmental
249 variation. However, as the purpose of structuring cohorts into separate groups was to
250 minimise within-group heterogeneity, not to explicitly test for relationships between tipulid
251 abundance and management impacts on survival, testing alternative formations of cohort
252 groupings (for example, grouping the relatively high tipulid abundance 2016-2017 year with
253 the 'good-survival' cohorts) is not appropriate. Further years of data would be required to
254 formally test whether intervention exposure and/or efficacy varied with tipulid abundance (or
255 with other environmental variables), especially since sample sizes of ringed choughs within
256 each cohort are too small to estimate cohort-specific parameters with high precision.

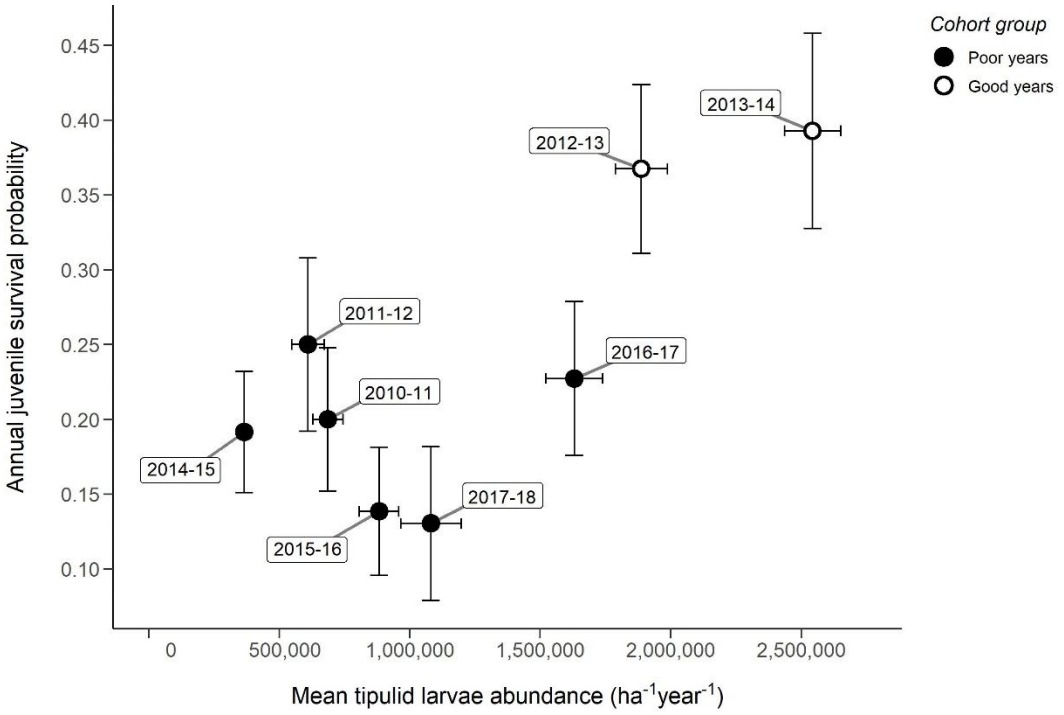


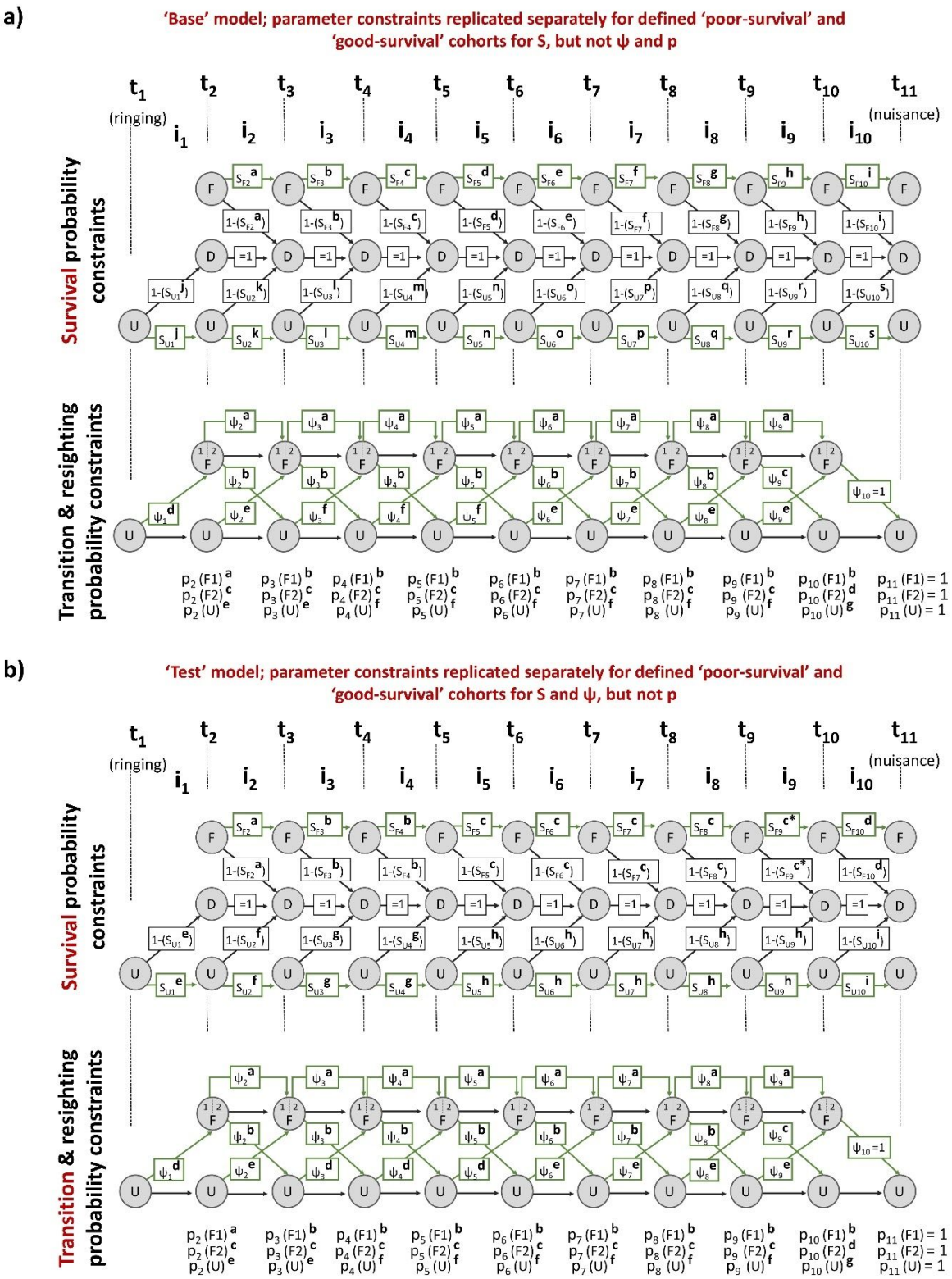
Figure S4: Cohort-groups used for multi-state analysis, structured into 'poor-survival' and 'good-survival' cohorts based on observed annual juvenile survival probabilities (±SE, labels denote cohort-year), and plotted against winter tipulid larvae abundance ($ha^{-1}year^{-1}$ mean±SE). Simple analyses across annual survival and tipulid abundance means that observed cohort annual survival probabilities were correlated with among-year variation in tipulid abundance (Pearson's correlation coefficient: r_6=0.77, adjusted R-squared=0.52).

Furthermore, there is no way to separate the potential impacts of parasite treatments from those of supplementary feeding. This is for several reasons. Firstly, all individuals that were treated for parasites post-fledging also attended supplementary feeding stations, precluding comparison between food supplemented and non-food supplemented individuals that received parasite treatments. Secondly, and most importantly, selection of individuals for

parasite treatment at feeding sites was highly non-random; treatment was specifically targeted at individuals that were visibly infected, and therefore most ill. Therefore, estimation of parasite treatment effects is not possible through direct comparison of fed individuals that did or did not receive parasite treatment. Finally, parasite treatments were only administered during 'poor-survival' years, and so no potential comparisons are possible between 'poor-survival' and 'good-survival' cohorts. Furthermore, comparing models with and without treated individuals would not be feasible, since removal of these individuals would further reduce the already small sample size available, and hence reduce the precision of parameter estimates of interest.

3.2.2 Initial constrained model structure: the 'Base Model'

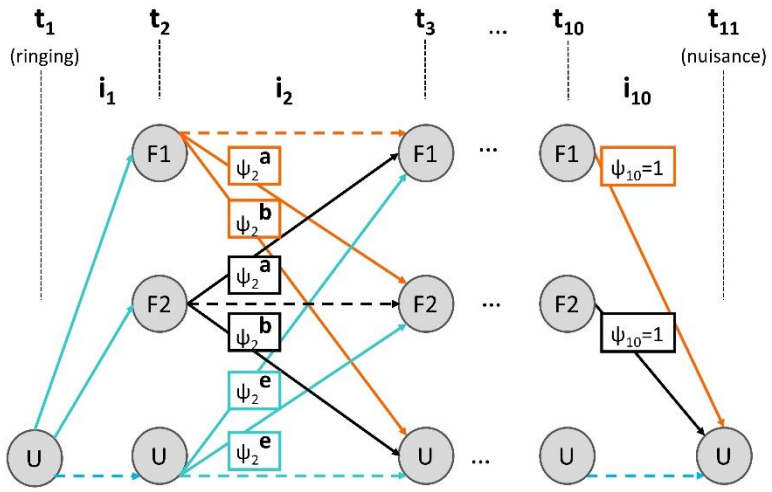
An initial constrained model (i.e., the Basel Model, Figure S5a), was fitted, which aimed to balance biological complexity with realistic parameter estimation given sample sizes (51 parameters to be estimated, 47 of them biologically meaningful: S=34, ψ=6, p=7; Figure S5). Constraints placed on survival, transition and resighting probabilities were primarily informed by expert knowledge of the system, and associated expectations of where rates may vary. Since the primary interest was to assess the global effect of the intervention on survival, rather than the site-specific effects, corresponding parameters for State-Fed-1 and State-Fed-2 were constrained to be equal, but no further within-year constraints were made for the Base Model (Figure S5a). However, since all individuals started in State-Unfed at t_1, there was no estimable survival probability associated with State-Fed over i_1, and so parameter values were fixed to an arbitrary value.



295

296 **Figure S5: Structure of the a) 'Base Model' and b) 'Test Model' multi-state mark-**
297 **recapture models. Individual encounter histories comprised of 11 encounter occasions**
298 **(t_1-t_{11}), and ten intervals (i_1-i_{10}) from colour-ringing in May, over which survival (S),**

transition (ψ) and resighting (p) probabilities could be estimated. Within-year constraints on survival, transition and resighting probability parameters, shown by superscript letter indices in bold (Base Model: S: a-s, ψ: a-f, p: a-g; Test Model: S: a-i, ψ: a-e, p: a-g). In practice transitions to, and between, the two feeding areas were considered (F1 and F2). In the Base Model, parameter constrains were replicated separately for 'poor-survival' and 'good-survival' cohorts for S, but not for ψ and p, while for the Test Model, constrains were replicated separately for S and ψ, but not p. Additionally, in the Test Model, S during i_9 was parameterised separately from i_5-i_8 for State-Fed in 'poor-survival' cohorts (asterisks). The final encounter occasion (t_{11}) is a nuisance parameter, describing whether an individual was seen alive past age one year; parameter estimates associated with t_{11} and i_{10} are not biologically meaningful. The numbers of biologically meaningful parameters were therefore: Base Model: S=34, ψ=6, p=7; Test Model: S=15, ψ=10, p=7. All individuals start in State-Unfed at ringing. Surviving individuals at t_{11} are constrained to remain in or transition to State-Unfed. Directly estimated S and ψ parameters are shown by green arrows. Other parameters (i.e. mortality probability, or ψ between the same state) were calculated as 1-probability of survival, or changing state, respectively (black arrows).



317

318 **Figure S6: Further details of transition probability structure between states in 'Base**
319 **Model' and 'Test Model' multi-state mark-recapture model. For simplicity, transitions**
320 **are only shown for a subset of intervals (i_1, i_2 and i_{10}). Transition probabilities are**
321 **possible between all three states (F1 = State-Fed-1, F2 = State-Fed-2, U = Unfed) during**
322 **all intervals (i_2-i_9), excluding the first (i_1) and last (i_{10}) where all individuals began in or**
323 **were constrained to transition to State-Unfed at t_1 and t_{11}, respectively. Parameters**
324 **were constrained to be equal between State-Fed-1 and State-Fed-2, i.e. State-Fed.**
325 **Transitions between states are depicted by coloured arrows (from State-Unfed = blue,**
326 **from State-Fed-1 = orange, from State-Fed-2 = black). Directly estimated ψ parameters**
327 **(ψ between different states) are shown by solid arrows. Inferred ψ parameters (ψ**
328 **between the same state) are shown by dashed arrows, and were calculated as 1-**
329 **probability of changing state. Within-year constraints indicated by letter indices.**

330

331 To facilitate initial model convergence, state-dependent p parameters were grouped
332 within years, for each state separately (Figure S5). Given the intensive resightings surveys
333 each May and throughout each year, we assumed all individuals alive past age one year
334 would be observed at some point, and therefore fixed p to equal one for the nuisance

parameter t_{11} across all three states. Due to the frequent high-intensity resighting effort at food-station-1 and food-station-3 (Table S1), p for State-Fed-1 was assumed to be constant through the year. However, as the exact dates on which supplementary feeding began each year varied slightly, the p associated with t_2 was estimated separately to allow for this. Therefore, three parameters were used to describe p associated with State-Fed-1: one for t_2, one for t_3-t_{10}, and one for the final 'nuisance' encounter occasion (t_{11}; fixed to one) (Figure S5). Resighting effort at food-station-2 was less intensive through most of the year, but intensive through the annual May census, so parameter constraints were set to capture expected variation in p. Specifically, we assumed that p was approximately constant between t_2 and t_9, but likely higher during t_{10}, associated with the annual census. Therefore, three parameters were used to describe p associated with State-Fed-2: one for t_2-t_9, one for t_{10}, and one for the final 'nuisance' encounter occasion (t_{11}; fixed to one) (Figure S5). Resighting effort of individuals not attending supplementary feeding (i.e. those in State-Unfed) was known to be inconsistent across the annual cycle, and so parameter constraints were set to capture some of this known variation. Firstly, effort to identify individuals on natal territories soon after fledging (in t_2 and t_3) was greater than later in the year. Subsequently, after most individuals had left natal territories for sub-adult flocking areas, we assumed an approximately constant resighting effort from t_4-t_9. Resighting effort may then differ during t_{10}, associated with the annual census. Therefore, four parameters were used to describe p associated with State-Unfed: one for t_2 and t_3, one for t_4-t_9, one for t_{10}, and one for the final 'nuisance' encounter occasion (t_{11}; fixed to one) (Figure S5). Since the consistent fieldwork protocols meant that there was no clear expectation that p for each of these three observed states would vary substantially between the eight cohorts, p parameters for each state were constrained to be equal between associated 'poor-survival' and 'good-survival' cohorts (Figure S5).

To further facilitate model convergence and parameter estimation, ψ were grouped among states, and within years (Figure S5). Firstly, as there was no expectation that analogous transition probabilities associated with State-Fed-1 or State-Fed-2 would differ substantially, we set ψ from State-Fed-1 to State-Fed-2 ($\psi^{F1\text{-}F2}$) equal to ψ from State-Fed-1 to State-Fed-2 ($\psi^{F2\text{-}F1}$), set ψ from State-Fed-1 to State-Unfed ($\psi^{F1\text{-}U}$) equal to ψ from State-Fed-2 to State-Unfed ($\psi^{F2\text{-}U}$), and ψ from State-Unfed to State-Fed-1 ($\psi^{U\text{-}F1}$) equal to ψ from State-Unfed to State-Fed-2 ($\psi^{U\text{-}F2}$)(Figure S5). However, as individuals at t_1 were assigned to State-Unfed, ψ from State-Fed across i_1 was fixed to zero. Then as all individuals were assigned to State-Unfed at t_1 and t_{11} (Figure S5), ψ from State-Fed was constrained to equal zero across i_1, ψ to State-Fed was constrained to equal zero across i_{10}, and ψ to State-Unfed was constrained to equal one across i_{10}. ψ during i_2-i_9 was then constrained within each state. As movement between supplementary feeding areas was infrequently observed, ψ between the two Fed states was assumed to be approximately constant through the year, and therefore constrained to be equal across i_2-i_9. Therefore, three parameters were used to describe ψ between the two Fed states: one for i_1 (fixed to zero), one for i_2-i_9, and one for the final 'nuisance' interval (i_{10}; fixed to one) (Figure S5). It was then assumed that ψ from State-Fed to State-Unfed (i.e. $\psi^{F1\text{-}U} = \psi^{F2\text{-}U}$) was approximately constant between i_2-i_8 (i.e. the period when food is generally more restricted), but as natural food abundance may be less limiting during i_9 (when *tipulid* larvae, in particular, become more available), or individuals may begin prospecting for territories away from feeding areas, ψ across i_9 was parameterised separately. Therefore, four parameters were used to describe ψ from the two Fed states to State-Unfed: one for i_1 (fixed to zero), one for i_2-i_8, one for i_9, and one for the final 'nuisance' encounter occasion (i_{10}; fixed to one) (Figure S5). ψ from State-Unfed to State-Fed was assumed to vary with key biological events, principally with large movement to feeding areas post-fledging (i_1), and with approximate periods of previously identified particularly low food

385 availability (i_3-i_5) (Reid et al., 2011). ψ from State-Unfed to State-Fed for the rest of the year
386 (i_2,i_6-i_9) was assumed to be approximately constant. Since only one individual was observed
387 in State-Unfed at t_9, ψ could not be estimated separately across i_9. Therefore, four parameters
388 were used to describe ψ from State-Unfed to State-Fed: one for i_1, one for i_2,i_6-i_9, one for i_3-i_5,
389 and one for the final 'nuisance' interval (i_{10}; fixed to zero) (Figure S5). For simplicity, ψ
390 parameters for corresponding 'poor-survival' and 'good-survival' cohorts were initially
391 constrained to be equal in the Base Model.

392

393 *3.2.3 Improving model fit: the 'Test Model'*

394 Some parameters were still poorly estimated in the Base Model, especially survival estimates
395 for State-Unfed (likely due to small sample sizes). Therefore, to improve precision of
396 estimates, and model parsimony, the Base Model was further refined by 1) further
397 simplifying parameterisation of ψ between State-Fed and State-Unfed, 2) simplifying
398 parameterisation of S for State-Unfed, 3) expanding parameterisation of ψ to reflect
399 differences between cohort-groups, and 4) simplifying parameterisation of S for State-Fed
400 (Table S3). This refined model, which then acts as the basis for hypothesis driven model
401 comparisons, is hereafter referred to as the 'Test Model' (Figure S5b, Figure 1 in main
402 manuscript).

403

Table S3: Summary of model refinement from the Base Model to the Test Model. Parameters: S = survival probability, and ψ = transition probability (for example, $\psi^{U\text{-}F}$ indicates transition probability from State-Fed to State-Unfed). Description (D) explains stepwise parameter constraints applied to each 'precursor model', that subsequently results in the corresponding 'constrained model'. Justification (J) explains the reason for these constraints, primarily based on expert knowledge of the system. k = number of estimable parameters contained in the model. -2lnL = Negative log-likelihood of the model. QAICc - Akaike's Information Criterion adjusted for sample size (AICc), and adjusted for overdispersion (QAIC). ΔQAICc shows difference between QAICc between Model and Precursor model.

Constrained model	Precursor model	Parameter type and state modified	Description (D) and justification (J)	k	-2lnL	QAICc	ΔQAICc
0.	-	-	Baseline model, with separate State-Fed-1, State-Fed-2 and State-Unfed states for survival parameters	69	1516.48	5148.56	NA
1. 'Base Model'	0.	S State-Fed	D: Combined State-Fed-1 and State-Fed-2 into an overall State-Fed J: Primary interest was assessing the global effect of the intervention on survival, rather than the site-specific effects.	51	1532.53	5126.75	-21.82
2.	1.	$\psi^{U\text{-}F}$	D: Constrain parameters corresponding to i_1 and i_3-i_5 to be equal	50	1532.70	5124.82	-1.92
3.	2.	$\psi^{U\text{-}F}$	D: Constrain $\psi^{U\text{-}F}$ parameters corresponding to t_3-t_{11} to be equal	49	1537.29	5127.33	2.51
4.	2.	S State-Unfed	D: Constrain parameters corresponding to i_3 and i_4 to be equal, and constrain parameters corresponding to i_5-i_8 to be equal J: Reid et al. (2011) found that generally, juvenile survival probability during years of low annual survival (2007-2009) was low in late summer (here, corresponding approximately to i_3 and i_4) compared to later in the annual cycle.	42	1536.94	5112.44	-14.89

			Therefore, for both 'poor-survival' and 'good-survival' cohorts: • S_1 as one parameter: expect that initial survival after fledging may be different to subsequent survival • S_2 as one parameter: may expect survival during this period to be different from survival during the rest of the annual-cycle • S_3 and S_4 as one parameter: corresponding to periods of previously identified lower within-year survival • S_5-S_8 as one parameter: corresponding to periods of previously identified greater within-year survival • S_9 as one parameter: previous research (Reid et al., 2011) suggests that survival from January onwards (i.e. during i_9) is relatively stable and high. However, it is plausible that survival may yet still be different during i_9 than either i_3-i_4 or i_5-i_8. • S_{10} as one parameter: nuisance parameter				
5.	4.	S State-Unfed	D: Combine parameter estimating S_9 for 'poor-survival' cohorts and parameter estimating S_9 for 'good-survival' cohorts to be equal. J: S_9 survival parameter was poorly estimated for both 'poor-survival' and 'good-survival' cohorts, presumably because of relatively low sample sizes. However, there was little reason to assume that survival during this period should be different for between 'poor-survival' and 'good-survival' cohorts; Reid et al. (2011) found little difference in survival during these months among years.	41	1536.94	5110.37	-2.07
6.	5.	S State-Unfed	D: Constrain parameter corresponding to S_9 to be equal to the parameter describing S_2 and S_5-S_8, for both 'poor-survival' and 'good-survival' cohorts, respectively. J: Coefficient corresponding to State-Unfed S_9 in Model 5 was still poorly estimated (for both 'poor-survival' and 'good-survival' cohorts), likely because there was limited data here. Therefore, to allow sensible parameter estimation, given that survival during i_9 was unlikely to be drastically different to that during i_8, S_9 was set	40	1538.07	5109.42	-0.95

			equal to S_8, for both 'poor-survival' and 'good-survival' cohorts separately.				
7.	6.	$\psi^{U\text{-}F}$	D: Split parameterisation of $\psi^{U\text{-}F}$ into 'poor-survival' and 'good-survival' cohorts. J: It was reasonable that transition probabilities may vary between 'poor-survival' and 'good-survival' cohorts. Logically, transitions from State-Unfed to State-Fed was a sensible starting point to assess if parameters corresponding to 'poor-survival' and 'good-survival' cohorts should be separate; if food was more limited in 'poor-survival' cohorts, individuals may transition at a greater rate from State-Unfed to State-Fed than in 'good-survival' cohorts.	42	1514.31	5089.81	-19.62
8.	7.	$\psi^{F\text{-}U}$	D: Split parameterisation of $\psi^{F\text{-}U}$ into 'poor-survival' and 'good-survival' cohorts. J: It was reasonable that transition probabilities may vary between 'poor-survival' and 'good-survival' cohorts.	44	1500.38	5080.03	-9.78
9.	8.	$\psi^{F\text{-}F}$	D: Split parameterisation of $\psi^{F\text{-}F}$ into 'poor-survival' and 'good-survival' cohorts. J: It was reasonable that transition probabilities may vary between 'poor-survival' and 'good-survival' cohorts.	45	1494.45	5076.17	-3.86
10.	9.	S State-Fed ('poor-survival' cohorts)	D: Constrain parameterisation of State-Fed survival in 'poor-survival' cohorts • S_1 as one parameter: Not possible given individual encounter history structuring, so value fixed (i.e. not estimated). • S_2 as one parameter: Survival here may different to subsequent periods • S_3 and S_4 as one parameter: Match structure of Unfed survival (see Model 4) • S_5-S_8 as one parameter: Match of Unfed survival (see Model 4)	41	1498.05	5071.48	-4.70

			• S_9 as one parameter: previous knowledge (Reid et al., 2011) suggests that survival from January onwards (i.e. here approximately corresponding to i_9) was relatively stable and high. Here, it is reasonable may be different from either the i_3-i_4 or i_5-i_8, as so initially kept as a separate parameter. • S_{10} as one parameter: a nuisance parameter				
11.	10.	S State-Fed (‘good-survival’ cohorts)	D: Constrain parameterisation of State-Fed survival in ‘good-survival’ cohorts, in the same fashion as survival parameters were constrained in Model 10	37	1501.93	5067.09	-4.39
12.	11.	S State-Fed (‘poor-survival’ cohorts)	D: For Constrain parameter for S_9 of ‘poor-survival’ cohorts equal to parameter for S_5-S_8 of ‘poor-survival’ cohorts. J: Test whether S_5-S_8 and S_9 were different, and therefore justify keeping them separately parameterised.	36	1504.59	5067.68	0.59
13.	11.	S State-Fed (‘good-survival’ cohorts)	D: For Constrain parameter for S_9 of ‘good-survival’ cohorts equal to parameter for S_5-S_8 of ‘good-survival’ cohorts. J: Test whether S_5-S_8 and S_9 were different, and therefore justify keeping them separately parameterised	36	1502.49	5065.59	-2.10

411

412

Table S4: Estimated coefficients for Test Model (i.e. model 13, Table S3). Model consists of 36 estimated parameters (32 biologically meaningful, 4 'nuisance'), and 15 fixed parameters. S = survival probability, p = resighting probability and ψ = transition probability. Poor = 'poor-survival' cohorts, good = 'good-survival' cohorts. Fixed and 'nuisance' parameters values and estimates are not presented. Note that as uneven time intervals were specified in the model, survival estimates are weekly survival probability.

Par. No.		Coefficient		Estimate	S.E.	Lower 95% CI	Upper 95% CI
1	S:	Fed^{Poor}	$[S_2]$	0.99	0.01	0.96	1.00
2	S:	Fed^{Poor}	$[S_3\text{-}S_4]$	0.94	0.01	0.92	0.95
3	S:	Fed^{Poor}	$[S_5\text{-}S_8]$	0.98	0.00	0.97	0.98
4	S:	Fed^{Poor}	$[S_9]$	0.99	0.00	0.98	0.99
5	S:	Fed^{Good}	$[S_2]$	0.98	0.01	0.94	1.00
6	S:	Fed^{Good}	$[S_3\text{-}S_4]$	0.97	0.01	0.95	0.98
7	S:	Fed^{Good}	$[S_5\text{-}S_9]$	0.99	0.00	0.98	0.99
8	S:	$Unfed^{Poor}$	$[S_1]$	0.91	0.01	0.87	0.93
9	S:	$Unfed^{Poor}$	$[S_2]$	0.97	0.01	0.94	0.99
10	S:	$Unfed^{Poor}$	$[S_3\text{-}S_4]$	0.91	0.02	0.87	0.94
11	S:	$Unfed^{Poor}$	$[S_5\text{-}S_9]$	0.91	0.02	0.86	0.95
12	S:	$Unfed^{Good}$	$[S_1]$	0.91	0.02	0.85	0.95
13	S:	$Unfed^{Good}$	$[S_2]$	1.00	0.00	1.00	1.00
14	S:	$Unfed^{Good}$	$[S_3\text{-}S_4]$	0.97	0.03	0.81	1.00
15	S:	$Unfed^{Good}$	$[S_5\text{-}S_9]$	0.99	0.01	0.29	1.00
16	ψ:	Fed-Fed^{Poor}	$[\psi_2\text{-}\psi_9]$	0.06	0.01	0.04	0.08
17	ψ:	Fed-Fed^{Good}	$[\psi_2\text{-}\psi_9]$	0.02	0.01	0.01	0.05
18	ψ:	Fed-$Unfed^{Poor}$	$[\psi_2\text{-}\psi_8]$	0.08	0.01	0.06	0.11
19	ψ:	Fed-$Unfed^{Poor}$	$[\psi_9]$	0.11	0.05	0.05	0.23
20	ψ:	Fed-$Unfed^{Good}$	$[\psi_2\text{-}\psi_8]$	0.06	0.01	0.04	0.09
21	ψ:	Fed-$Unfed^{Good}$	$[\psi_9]$	0.43	0.09	0.28	0.61
22	ψ:	Unfed-Fed^{Poor}	$[\psi_1, \psi_3\text{-}\psi_5]$	0.30	0.02	0.26	0.34
23	ψ:	Unfed-Fed^{Poor}	$[\psi_2, \psi_6\text{-}\psi_9]$	0.23	0.03	0.19	0.29

24	ψ:	Unfed-Fed^{Good}	$[\psi_1, \psi_3\text{-}\psi_5]$	0.40	0.02	0.36	0.44
25	ψ:	Unfed-Fed^{Good}	$[\psi_2, \psi_6\text{-}\psi_9]$	0.43	0.04	0.35	0.51
26	p:	Fed-1	$[p_2]$	0.83	0.04	0.72	0.90
27	p:	Fed-1	$[p_3\text{-}p_{10}]$	1.00	0.00	1.00	1.00
28	p:	Fed-2	$[p_2\text{-}p_9]$	0.34	0.02	0.30	0.39
29	p:	Fed-2	$[p_{10}]$	0.67	0.09	0.47	0.82
30	p:	Unfed	$[p_2\text{-}p_3]$	0.83	0.06	0.68	0.92
31	p:	Unfed	$[p_4\text{-}p_9]$	0.87	0.07	0.68	0.95
32	p:	Unfed	$[p_{10}]$	0.66	0.13	0.39	0.86

3.2.4 Hypothesis driven model comparisons

A series of hypotheses regarding difference in survival of State-Fed and State-Unfed over time were tested, by comparing the Test Model (Figure 1 in main manuscript, Figure S5b, Model 13 in Table S3; Table S4) to a series of nested models (Table S5).

425 **Table S5: Comparison of hypothesis driven candidate mark-recapture models. The Test Model was used as a basis for all subsequent**
426 **comparison models. Description (D) explains parameter constraints applied to the 'Test Model' to achieve the 'Nested Model', and**
427 **Conclusion (C) explains the conclusion reached from comparing the Nested model to the Test Model, based on the ΔQAICc. k = number**
428 **of estimable parameters contained in the model. -2lnL = Negative log-likelihood of the model. ΔQAICc values indicate the difference in**
429 **QAICc (Akaike Information Criterion adjusted for small sample size and model overdispersion) between the Test Model and a nested**
430 **model. Negative ΔQAICc values indicate that a nested model was more parsimonious that the Test Model. Models were considered**
431 **relatively better supported than alternative candidate models if ΔQAICc > 2 (i.e. if value in ΔQAICc column < -2, model better supported**
432 **than the Test Model).**

Model	State	Cohort (group)	Description (D) and Conclusion (C)	k	-2lnL	QAICc	ΔQAICc
'Test Model'	-	-	-	36	1502.49	5065.59	NA
Nested models	**1) Survival during i_3-i_4 (previously identified period of lower survival) is different from survival during i_5-$i_{8/9}$ (previously identified period of higher survival)**						
A	Fed	'Poor-survival' cohorts	M: Constrain the two parameters corresponding to State-Fed S_3-S_4 and State-Fed S_5-S_8 in 'poor-survival' cohorts to be equal. C: Model is substantially better supported when S_3-S_4 and S_5-S_8 are parameterised separately.	35	1518.32	5079.36	13.77
B	Fed	'Good-survival' cohorts	M: Constrain the two parameters corresponding to State-Fed S_3-S_4 and State-Fed S_5-S_9 in 'good-survival' cohorts to be equal.	35	1508.32	5069.36	3.77

			C: Model is substantially better supported when S_3-S_4 and S_5-S_9 parameters are parameterised separately.				
C	Unfed	'Poor-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_3-S_4 and State-Unfed S_5-S_9 in 'poor-survival' cohorts to be equal. C: Model is substantially better supported when critical and non-critical months are constrained to be equal.	35	1502.50	5063.54	-2.05
D	Unfed	'Good-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_3-S_4 and State-Unfed S_5-S_9 in 'good-survival' cohorts to be equal. C: Model is moderately better supported when S_3-S_4 and S_5-S_9 parameters are constrained to be equal.	35	1503.09	5064.13	-1.46
	2) Survival during i_3-i_4 (previously identified period of lower survival) is different between State-Unfed and State-Fed						
F	Unfed and Fed	'Poor-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_3-S_4 and State-Fed S_3-S_4 in 'poor-survival' cohorts to be equal. C: Model is marginally better supported when State-Unfed and State-Fed survival during the critical months in 'poor-survival' cohorts are parameterised separately ($0<\Delta QAICc<+2$). However, a difference between State-Unfed and State-Fed survival here may be unclear due to the low estimate precision for State-Unfed survival.	35	1504.74	5065.77	0.19
G.a and G.b	Unfed and Fed	'Poor-survival' cohorts	State-Unfed survival during i_3-i_4 was estimated with relatively poor precision compared to other survival estimates, and therefore, it is plausible that a difference between State-Unfed and State-Fed survival is hidden because of this. M: Model estimates of State-Unfed S_3-S_4 and State-Unfed S_5-S_9 in 'poor-survival' cohorts were very similar (both 0.91, see Table S4). To increase estimate precisions, parameters for State-Unfed S_3-S_4 and State-Unfed S_5-S_9 were constrained to be equal (Model G.a), and then State-Unfed S_3-S_9 and State-Fed S_3-S_4 were constrained to be equal (Model G.b).	a) 35 b) 34	1502.50 1506.01	5063.54 5064.99	NA 1.45

			Assessment of whether there was a difference between State-Unfed and State-Fed during the critical months is thereby based on a comparison between Model G.a and Model G.b. C: Model is marginally better supported when State-Unfed survival during i_3-i_9 and State-Fed survival during i_3-i_4 in 'poor-survival' cohorts are parameterised separately.				
H	Unfed and Fed	'Good-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_3-S_4 and State-Fed S_3-S_4 in 'good-survival' cohorts to be equal. C: Model is substantially better supported when parameters for State-Unfed and State-Fed survival during i_3-i_4 in 'good-survival' cohorts are constrained to be equal.	35	1502.50	5063.54	-2.05
	3) Survival during i_5-$i_{8/9}$ (previously identified period of higher survival) is different between State-Unfed and State-Fed						
I	Unfed and Fed	'Poor-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_5-S_9 and State-Fed S_5-S_8 in 'poor-survival' cohorts to be equal. C: Model is substantially better supported when parameters for State-Unfed and State-Fed survival during i_5-$i_{8/9}$ are parameterised separately.	35	1515.83	5076.87	11.28
J	Unfed and Fed	'Good-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_5-S_9 and State-Fed S_5-S_9 in 'good-survival' cohorts to be equal. C: Model is marginally better supported when parameters for State-Unfed and State-Fed survival during i_5-i_9 in 'good-survival' cohorts are constrained to be equal.	35	1502.70	5063.73	-1.85
	4) Survival during i_5-$i_{8/9}$ in State-Unfed and State-Fed in 'good-survival' cohorts is different to State-Fed survival in the 'poor-survival' cohorts						
L	Unfed and Fed	'Poor-survival' and 'good-survival' cohorts	M: Constrain parameters for State-Unfed S_5-S_9 and State-Fed S_5-S_9 in 'good-survival' cohorts and State-Fed S_5-S_8 in 'poor-survival' cohorts to be equal.	34	1509.04	5068.02	2.44

			C: Model is substantially better supported when State-Unfed and State-Fed survival in 'good-survival' cohorts and State-Fed survival in 'poor-survival' cohorts during i_5-$i_{8/9}$ are parameterised separately.				
	5) Survival during early summer (i.e. survival across i_2; S_2) is different between State-Unfed and State-Fed						
M	Unfed and Fed	'Poor-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_2 and State-Fed S_2 in 'poor-survival' cohorts to be equal. C: Model is marginally better supported when State-Unfed and State-Fed survival parameters corresponding i_2 in 'poor-survival' cohorts is constrained to be equal.	35	1503.47	5064.51	-1.08
N	Unfed and Fed	'Poor-survival' and 'good-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_2 and State-Fed S_2 in 'good-survival' cohorts to be equal. C: Model is marginally better supported when State-Unfed and State-Fed survival parameters corresponding to i_2 in 'good-survival' cohorts are constrained to be equal.	35	1503.00	5064.04	-1.54
	6) Post-fledging survival (i.e. survival across i_1; S_1) is different between 'poor-survival' and 'good-survival' cohorts						
O	Unfed	'Poor-survival' and 'good-survival' cohorts	M: Constrain the two parameters corresponding to State-Unfed S_1 in 'poor-survival' cohorts and 'good-survival' cohorts to be equal. C: Model is better supported when survival parameters corresponding to i_1 is constrained to be equal across 'poor-survival' and 'good-survival' cohorts	35	1502.52	5063.56	-2.03

433

434

435 3.3 Model checking; checking for overdispersion, and for multiple maximums in the
436 likelihood function
437 Both the Base and Test Models showed relatively little overdispersion, and hence little
438 evidence of major lack of fit (median variance inflation factor $\hat{c}$±SE: Base Model=1.23±0.01,
439 Test Model=1.17±0.01, Appendix 3). $\hat{c}$ for subsequent nested models built to test specific
440 hypotheses was set to 1.23. Model comparisons were therefore made using Akaike's
441 information criterion corrected for overdispersion, as well as small sample size (QAICc).

442 Multi-state models sometimes encounter issues with multiple maximums in the
443 likelihood function, which consequently potentially produces inaccurate estimates. To ensure
444 that the Test Model estimates reflect those at the global maximum of the likelihood, MCMC
445 was run for the Test Model (tune-in samples = 4000, burn-in samples = 1000, samples stored
446 from posterior = 10000, 10 chains) to confirm that model estimates reflected values at
447 maximum likelihood, rather than of a local minima. If Markov chains have converged
448 properly, values of Gelman-Rubin diagnostic ($\hat{R}$) should be 1.0, and Gelman (1996)
449 recommends that $\hat{R}$ values for all estimated parameters should be <1.2. Here, values of $\hat{R}$ for
450 all the estimated parameters was < 1.002, thereby indicating proper convergence, and a lack
451 of multiple maxima.

452

453

454 3.4 Summary and comparison of survival estimates

455

456 **Table S6: Comparisons and absolute differences for key comparisons of state- and group-**
457 **dependent survival probabilities across each interval, as visualised in Figure 2d&e. Values in**
458 **brackets show 95% confidence intervals. Note that some intervals are of different lengths**
459 **(Appendix 3.1.1), and therefore intervals i_5 to i_8 are kept separate here from i_9.**

Comparison			Survival probabilities	Absolute difference
State	Cohort-group	Intervals		
Comparisons between states within cohort-groups				
Fed vs Unfed	Poor	i_2	0.95 (0.89-0.99) vs 0.90 (0.80-0.97)	0.05
Fed vs Unfed	Good	i_2	0.93 (0.84-0.99) vs 1.00 (1.00-1.00)	0.07
Fed vs Unfed	Poor	i_3-i_4	0.78 (0.72-0.84) vs 0.70 (0.59-0.80)	0.09
Fed vs Unfed	Good	i_3-i_4	0.88 (0.82-0.94) vs 0.87 (0.62-0.999)	0.01
Fed vs Unfed	Poor	i_5-i_8	0.91 (0.87-0.94) vs 0.69 (0.55-0.82)	0.22
Fed vs Unfed	Good	i_5-i_8	0.95 (0.93-0.98) vs 0.94 (0.73-0.999)	0.01
Fed vs Unfed	Poor	i_9	0.81 (0.70-0.90) vs 0.26 (0.11- 0.46)	0.55
Fed vs Unfed	Good	i_9	0.84 (0.75-0.91) vs 0.82 (0.30-0.999)	0.02
Comparisons within states across the year				
Fed	Poor	i_3-i_4 vs i_5-i_8	0.78 (0.72-0.84) vs 0.91 (0.87- 0.94)	0.12
Unfed	Poor	i_3-i_4 vs i_5-i_8	0.70 (0.59-0.80) vs 0.69 (0.55-0.82)	0.01
Fed	Good	i_3-i_4 vs i_5-i_8	0.88 (0.82-0.94) vs 0.95 (0.93-0.98)	0.07
Unfed	Good	i_3-i_4 vs i_5-i_8	0.87 (0.62-0.999) vs 0.94 (0.73-0.999)	0.07

Comparisons within states between cohort-groups				
Unfed	Poor vs Good	i_1	0.82 (0.77-0.87) vs 0.82 (0.73-0.91)	-0.01

460

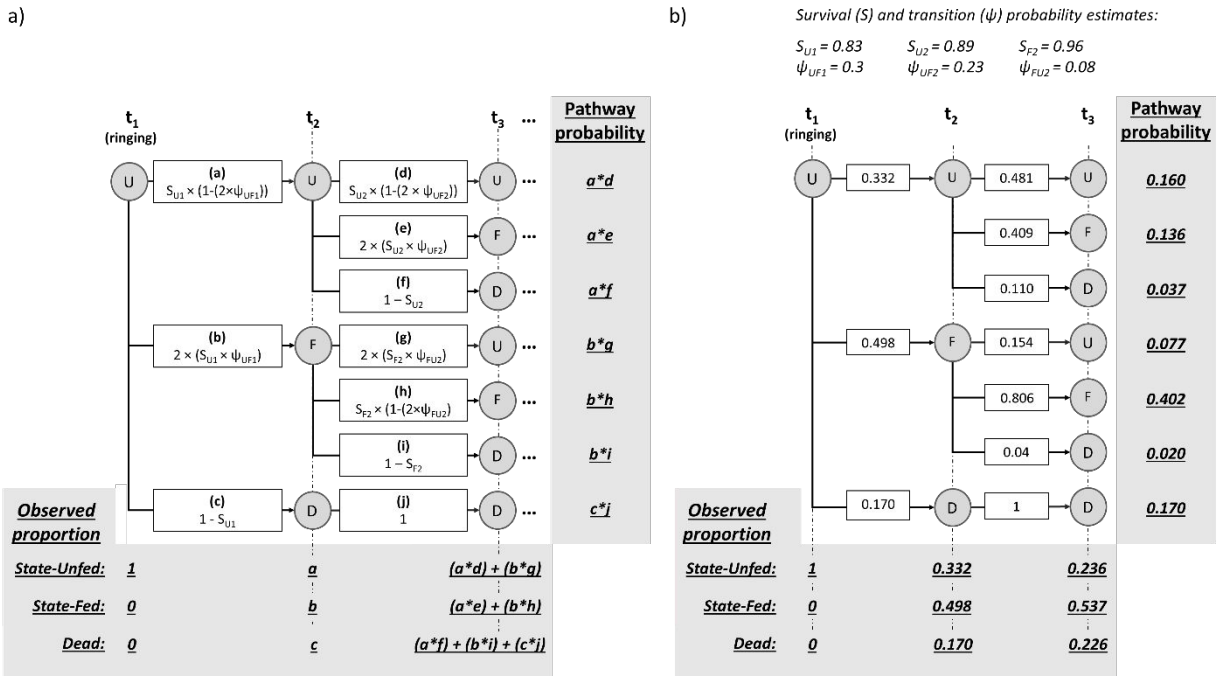
461

462 **Appendix S4. Calculating the probabilities of all possible pathways**

463 To estimate the proportions of individuals alive in State-Fed versus State-Unfed at each
464 occasion, state-dependent S and ψ estimates from the Test Model were used to calculate the
465 probabilities of all potential pathways of exposure and survival through the full annual cycle,
466 for both 'poor-survival' and 'good-survival' years.

467 All individuals began in State-Unfed at t_1. At each occasion, individuals may either
468 survive and remain within the same observable state (State-Unfed or State-Fed), survive and
469 move to a different observable state, or die and consequently move to the unobservable Dead
470 state, according to state- and time-dependent S and ψ (Figure S7a). Since there were two
471 underlying Fed states (State-Fed-1 and State-Fed-2) which were constrained to be equal (i.e.
472 State-Fed), estimated ψ to and from State-Fed were doubled. Individuals that transitioned to
473 the Dead state (i.e. died) cannot subsequently transition back to an observed 'alive' state, and
474 therefore the probability of remaining within the Dead state was set to 1. Consequently, over
475 the ten encounter occasions ($t_1 - t_{10}$) used in the analyses, there were 1023 different potential
476 pathways.

477



478

479 **Figure S7: Conceptualisation (a) and example (b) of calculating the probability of all possible**
480 **pathways, and resulting expected state-based frequencies of individuals across time.**
481 **Calculations used survival (S) and transition (ψ) probability values estimated from a multi-state**
482 **mark-recapture model for each observable state (U = State-Unfed, F = State-Fed), and inferred**
483 **estimates of a Dead state (D). For simplicity, pathways are only depicted up until the third**
484 **encounter occasion (t_3), rather than up to the tenth (t_{10}) as used in the full analyses. Estimated**
485 **values of ψ to and from State-Fed were doubled to account for transitions to and from the**
486 **underlying State-Fed-1 and State-Fed-2. Subscript letters indicate the state, and numbers**
487 **indicate the encounter occasion; e.g. ψ_{UF1} = ψ from State-Unfed to State-Fed during the first**
488 **interval. Letter indices show multiplications of parameters to calculate pathway probabilities**
489 **and expected state-based frequencies at each occasion.**

490

491 Using the example shown in Figure S7b, seven pathways are possible over the three-
492 occasion history. At t_2, approximately 83% of individuals alive at t_1 are estimated to be alive
493 (33% in State-Unfed, 50% in State-Fed), and 17% are estimated to be dead. At t_3,
494 approximately 78% of those individuals alive at t_1 are estimated to still be alive (24% in

State-Unfed [0.160 + 0.077], 54% in State-Fed [0.136 + 0.402]), and 17% are estimated to be dead (0.037 + 0.020 + 0.170). The most frequent pathway, accounting for approximately 40% of individuals alive at t_1, was that where individuals transitioned to State-Fed at t_2, and remained in State-Fed at t_3.

Appendix S5. Further details of population size projection over intervention period

To assess how the effects of the supplementary feeding and parasite treatment intervention on juvenile survival may have impacted population size over the intervention period, Lefkovitch matrices, assuming a pre-breeding census and birth-pulse dynamics, were constructed. Matrices comprised of four stage classes: age one, age two, age three and adult (ages ≥ four years, following Reid et al., 2004, 2011; Figure S8). Since the objective here was to evaluate the population-level consequences of management on juvenile survival, all other vital rates were set to constant baseline values (Table S7), based on values used by Reid et al. (2011).

To set an initial population size vector, an approximate initial population size for each age class at the start of the intervention period was estimated, since direct counts were not possible because not all individuals in the population are colour-ringed. To account for the differing numbers of fledglings ringed in each year, first-year, second-year and third-year population sizes was estimated as the population-wide breeding success in their natal year (i.e. breeding pairs multiplied by average breeding success), multiplied by successive age-structed estimates of survival for corresponding years estimated from independent capture-mark-recapture models (e.g. second-year population size estimated as 2008 number of pairs × 2008 average breeding success × 2008 juvenile survival × 2009 second-year survival). The number of individual adults was approximately estimated as twice the number of breeding pairs, which was known each year due to comprehensive population censuses. Initial population size in each age-category was consequently set as: first-year =14, second-year =5, third-year =3, adult = 86. Estimated population size of first-year and second-year individuals were broadly similar to direct counts of individuals in non-breeding flocks.

This initial population size vector was then multiplied by a Lefkovitch matrix parameterised with vital rates for ‘poor-survival’ cohorts. Thereafter, the resulting population size vector from the previous year was multiplied by matrices parameterised with vital rates

524 for ‘poor-survival’ cohorts or ‘good-survival’ cohorts, following the observed sequence of
525 ‘poor-survival’ or ‘good-survival’ cohorts (i.e. one ‘poor-survival’ cohort, then two ‘good-
526 survival’ cohorts, then four ‘poor-survival’ years). As one-year-old choughs have never been
527 observed to successfully breed on Islay, the probability of breeding aged one was set to zero.
528 An equal sex ratio was assumed, and so matrix fecundity terms were multiplied by 0.5.

529

530 **Figure S8. Four stage-class Lefkovitch matrix for projecting chough population size**
531 **over the intervention period. Terms are defined in Table S7.**

0	**$\frac{1}{2}(c_2 m_2 \phi_1)$**	**$\frac{1}{2}(c_3 m_3 \phi_1)$**	**$\frac{1}{2}(c_{ad} m_{ad} \phi_1)$**
ϕ_2	**0**	**0**	**0**
0	**ϕ_{ad}**	**0**	**0**
0	**0**	**ϕ_{ad}**	**ϕ_{ad}**

532

533

534 **Table S7. Definitions of matrix projection model terms and specified parameter values.**

535 **Fixed value parameters are equal to values used in Reid et al. (2011).**

Parameter	Definition	Value
	Fixed value parameters	
ϕ_2	Second-year survival probability (age one to age two)	0.63
ϕ_{ad}	Adult survival probability (age two year and older)	0.80
c_2	Probability that a two year-old will breed	0.28
c_3	Probability that a three year-old will breed	0.81
c_{ad}	Probability that an adult will breed	1.00
m_2	Breeding success (number of fledglings produced) of a two year-old	1.20
m_3	Breeding success (number of fledglings produced) of a three year-old	1.50
m_{ad}	Breeding success (number of fledglings produced) of an adult	2.0
	Variable value parameters	
ϕ_1	Juvenile survival probability (ringing to age one)	See Table S8

536

537 **Table S8: Mean and variance values of estimated first-year annual survival used for**

538 **sampling demographic rate values for matrix projection models.**

Pathway	Cohort-group	Mean	Variance
'Realised' scenario	Poor	0.16	0.017
	Good	0.42	0.040
'Worst-case' scenario	Poor	0.02	0.013
	Good	0.40	0.140
'Best-case' scenario	Poor	0.26	0.026
	Good	0.42	0.045

539

To approximate 95% confidence intervals (95%CIs) for realised and hypothetical scenarios, parameter value ranges corresponding to a normal distribution of estimates of survival probabilities and associated error from the Test Model were sequentially multiplied to generate monthly and annual survival estimates, and this sampling process repeated 10,000 times. The 2.5th and 97.5th percentiles of these survival values were used as the proximate confidence intervals.

These population matrix multiplications effectively achieve our objective of understanding how population size may have changed resulting from management impacts on juvenile survival. Integrated population models (IPMs) are an alternative method used to estimate changes in population size, particularly when not all demographic data are available. However, an IPM would not directly facilitate our current objectives. These were not to estimate real population change or size, or to understand how variability in all demographic rates may influence estimation of population size, but rather to estimate the hypothetical changes in population size resulting solely from changes in the target demographic of juvenile survival. However, future research on the chough system could potentially benefit from the advantages brought by IPMs.

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